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Middle Cambrian agnostoids and trilobites from the Lower Allochthon, Swedish Caledonides

Thomas Weidner, Arne Thorshøj Nielsen and Jan Ove R. Ebbestad

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Cover picture: Pygidium of *Kootenia* sp. from the *Acidusus atavus* Zone at Strömnäs (PMU 22839).

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by

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A middle Cambrian (Miaolingian) agnostoid-paradoxidid fauna from the Alum Shale Formation of the Lower Allochthon in the Caledonides of northwestern Sweden is described. More than 1000 specimens were collected from 46 localities in the Blaik Nappe Complex. This complex represents displaced strata, originally deposited on the distal outer shelf of Baltica. Strong tectonic overprint prevented systematic bed-by-bed sampling, but the collected fauna represents the *Pentagnostus praecurrens*, *Triplagnostus gibbus*, *Acidusus atavus*, *Ptychagnostus punctuosus*, *Goniagnostus nathorsti* and lower part of the *Lejopyge laevigata* agnostoid zones. The Hawke Bay hiatus encompasses the Kibartian and basal Bödan stages. Higher up, the upper part of the *L. laevigata* Zone appears to be absent, and the overlying *Agnostus pisiformis* Zone is found only at a few localities, developed as the Exporrecta Conglomerate. This is suggestive of local isostatic uplift in the late Miaolingian. One new species, *Cotalagnostus greilingi* n. sp., is described and *Lejopyge calva* Robinson, *Hypagnostus clipeus* Whitehouse, *Doryagnostus deltoides* Robinson and *Lisogoragnostus confluentus* (Rudolph) are for the first time reported from Sweden. All other taxa recorded are known also from the Miaolingian of southern Scandinavia, but the faunal composition in terms of relative frequencies differs. Agnostoid arthropods dominate (39 taxa) with trilobites (17 taxa) as a minor to rare constituent. The palaeoecology of Miaolingian faunas described from Scandinavia is discussed briefly. Three benthic biofacies are recognized, representing a depth transect from well-ventilated inner shelf environments dominated by a diverse trilobite fauna with sparse to infrequent agnostoids (southern Scandinavia) to outer shelf dysoxic environments with more frequent agnostoids and sparse to no trilobites (study area). ☐ *Agnostoids, Trilobites, Miaolingian, Cambrian, Lower Allochthon, Blaik Nappe Complex, Sweden.*

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Introduction

Strata of Cambrian age are widely distributed in Scandinavia (Fig. 1). The autochthonous Miaolingian ('Middle Cambrian', see Nielsen & Ahlberg 2019) of southern and central Sweden (Scania, Öland, Västergötland, Östergötland and Närke) is developed as the Borgholm and Alum Shale formations and comprises siltstones, mudstones, sandstones and shales, the latter with common bituminous limestone concretions (for lithostratigraphic details, see Nielsen & Schovsbo 2007). A few thin limestone horizons and conglomerates also occur (viz. Forsemölla, Exsulans, Hyolithes and Andrarum limestone beds and the Exporrecta Conglomerate Bed). These widespread highly fossiliferous marker beds have been used for inter-regional correlation across Scandinavia. The Cambrian sediments preserved east of the Caledonian mountain range are in most places almost undisturbed and essentially flat-lying, except in impact craters. The strata can be studied in coastal and river sections as well as in abandoned quarries, and fossils have also been reported from glacial erratics in Germany and Denmark. The bio- and chronozones established for the Scandinavian Miaolingian are based on the comparatively thick sequences present in Scania and on

Öland. The three superzones *Acadoparadoxides oelandicus*, *Paradoxides paradoxissimus* and *Paradoxides forchhammeri* (Fig. 2), are recognized and their faunas have received considerable attention over the years (Linnarsson 1869, 1873, 1877, 1879, 1883; Tullberg 1880; Wiman 1906; Wallerius 1894, 1895, 1896, 1930; Westergård 1936, 1942, 1944, 1946, 1948, 1950, 1953). From Norway and Bornholm, Denmark, Brøgger (1878) and Grönwall (1902), respectively, pioneered description of the 'Middle Cambrian'. For a more complete list of references, see Appendix 1. Trilobites, agnostoids, hyoliths, brachiopods and molluscs make up a rich and varied Baltic fauna, which is related closely to the faunas of eastern and western Avalonia (i.e. England & Wales, maritime eastern Canada & USA) and some genera or even species are shared with Siberia, Bohemia and Australia (Westergård 1946; Weidner & Nielsen 2014).

Along the Caledonian thrust front, a narrow strip of autochthonous Cambrian can be traced from southernmost Norway via western Sweden up to Finnmark in northern Norway (Fig. 1). This almost flatlying succession was deposited in an epicontinental sea facing open waters (the Iapetus Ocean) to the present day west. In Sweden, scattered findings of Cambrian Series 2 faunas are known from several localities along the Caledonian front (Moberg 1908; Kautsky 1945; Ahlberg & Bergström 1978, 1983; Ahlberg 1980, 1981, 1984, 1985; Ahlberg *et al.* 1986; Moczydłowska *et al.* 2001; Axheimer *et al.* 2007; Cederström *et al.* 2011, 2012; Nielsen & Schovsbo 2011; see the latter publication for a review). In central Jämtland, the

Fig. 1. Map of Scandinavia showing areas with well-studied Cambrian exposures. The rectangle encloses the investigated area in Jämtland, Ångermanland and Lapland, western Sweden, between Ströms Vattudal (lower dot) in the south and Hornavan (upper dot) in the north.

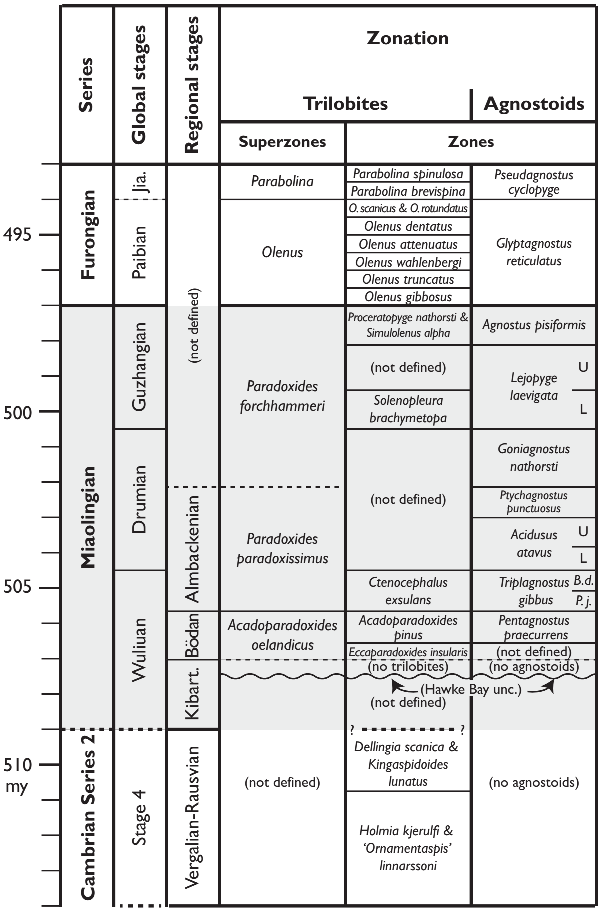


Fig. 2. Biozonation of the Miaolingian and adjacent strata. Based on Nielsen & Ahlberg (2019) with minor adjustments introduced by Nielsen *et al.* (2020). Abbreviations: Kibart., Kibartian; Jia., Jiangshanian; U and L, upper and lower; B.d., *Bailiaspis dalmani*; P.j., *Paradoxides jemtlandicus.*

autochthonous strip becomes wider and strata are well-exposed at many places (Fig. 3).

Here the Miaolingian is stratigraphically incomplete with only the *Acadoparadoxides pinus – Pentagnostus praecurrens* Zone (*A. oelandicus* Superzone), the *Triplagnostus gibbus* Zone (*P. paradoxissimus* Superzone) and a thin Exporrecta Conglomerate Bed representing the *Lejopyge laevigata* Zone (*P. forchhammeri* Superzone) proven present. Contrary to regions in southern Scandinavia, faunal studies of the Miaolingian in Jämtland are few (Wiman 1903; Asklund 1938; Thorslund 1940; occasional references in Westergård 1946, 1948, 1950, 1953). New studies and extensive collecting over the past 15 years, especially from the *A. pinus – P. praecurrens* Zone, have added considerably to the faunal record (Karis 1998; Axheimer 2006; Rushton 2006; Rushton & Weidner 2007; Ebbestad *et al.* 2013; Weidner & Ebbestad 2014; Rushton *et al.* 2016). Paradoxidid trilobites in Jämtland's *A. pinus – P. praecurrens* Zone attain their greatest diversity in Scandinavia, but the Miaolingian faunas as a whole are of much lower diversity than in southern Sweden. Further north, in the greater Storuman and Laisvall areas (Fig. 4), the 'lower' Cambrian is overlain by Alum Shale of supposed Miaolingian age (Ahlberg 1983; Moczydłowska *et al.* 2001; Nielsen & Schovsbo 2015), but this has not been confirmed by palaeontological evidence as yet. Also, on Mount Luobákti (older spelling Luopakte) in the Torneträsk area of northern Lapland, fossiliferous 'lower' Cambrian shales and limestones are overlain by Alum Shale of unknown age (Martinsson 1974; Ahlberg 1980; Nielsen & Schovsbo 2015). Even further north, in the Norwegian part of the mountain chain, Alum Shale of assumed Miaolingian age is preserved sporadically below the sole thrust (Nielsen & Schovsbo 2011 and references therein) but fossils have been recorded only from the Digermul Peninsula (Welsch 1986; Nikolaisen & Henningsmoen 1990; Palacios *et al.* 2020).

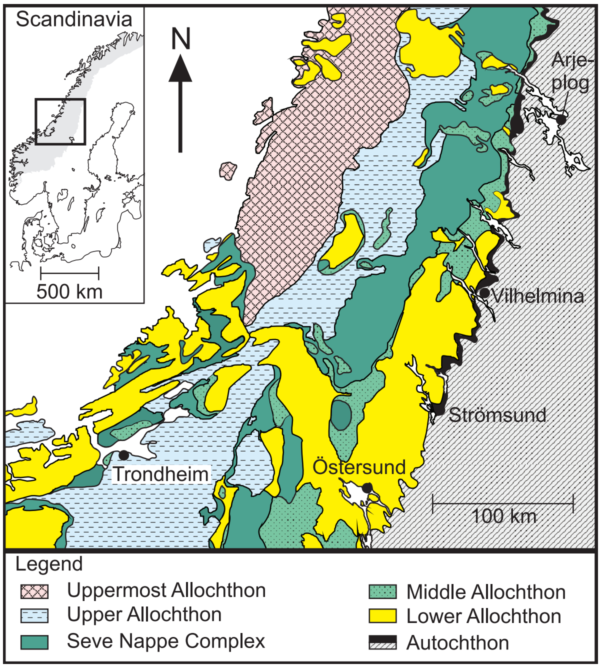


Fig. 3. Map of the central part of the Caledonian Mountain Range. It shows the narrow strip of autochthon strata, the Caledonian front and the different allochthonous units. The Blaik Nappe Complex represents the eastern marginal areas of the Lower Allochthon between Östersund and Arjeplog. North of Vilhelmina, the Blaik Nappe Complex is exposed only in windows in the Middle Allochthon. Modified from Angerer & Greiling (2012).

The Cambrian strata originally covered an area stretching several hundred kilometres west of the present-day Caledonian Front. These successions

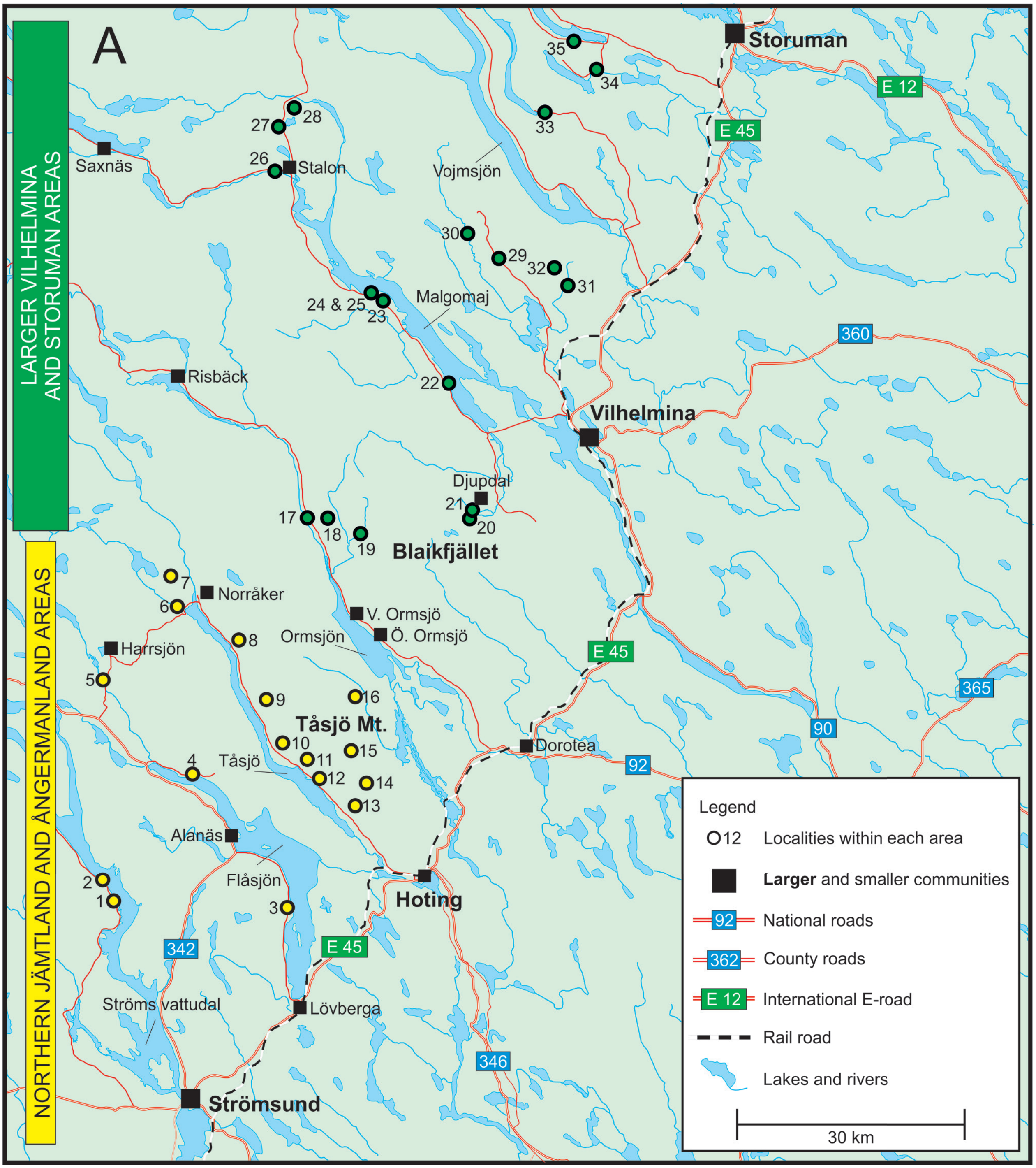


Fig. 4A. Map of the localities in northern Jämtland and the Tåsjö Mountain area (Ångermanland), in yellow. Localities in the larger Vilhelmina and Storuman areas of southern Lapland (Västerbotten), in green. The numbers refer to the localities listed in Table 1.

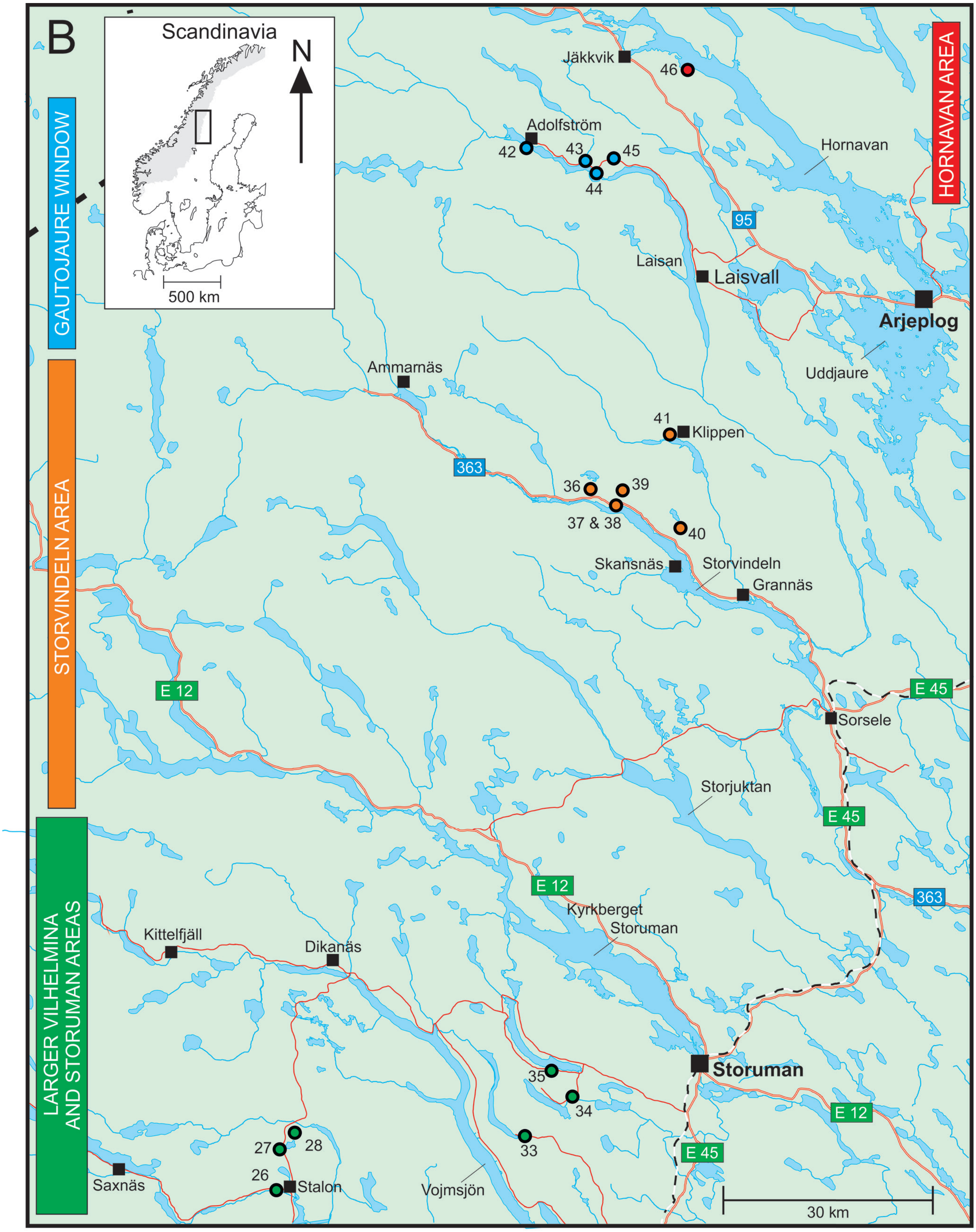


Fig. 4B. Localities at Storvindeln in southern Lapland (Västerbotten), in brown. Localities in the Gautojaure Window in northern Lapland (Norbotten), in blue. Localities at Lake Hornavan in northern Lapland (Norbotten), in red. The numbers refer to the localities listed in Table 1.

were telescoped and stacked into the mountain range during the Caledonian Orogeny. The Lower Allochthon nappes can be followed in Sweden from Härjedalen northward to Lapland (Fig. 3) and occasionally their original sedimentary succession can be reconstructed. Where exposed in windows west of the Caledonian front, the strata, and notably the Alum Shale, when preserved, are strongly overprinted by tectonism. Fossiliferous 'lower' Cambrian, Miaolingian and Furongian strata have been recorded at various localities in the so-called Blaik Nappe Complex (henceforth BNC). This complex includes all units beneath the higher allochthons in the eastern marginal area (Kulling 1955, 1972) (Fig. 5). From the Miaolingian west of Lake Storsjön in central Jämtland, several superzones and zones and some key trilobites and agnostoids were listed by Karis (1998). Comprehensive descriptions of localities and faunas have been compiled for northern Jämtland and the adjacent Tåsjö Mountain in Ångermanland by Asklund & Thorslund (1935), Asklund (1938) and Weidner *et al.* (2014). However, from the scattered localities between Ormsjön and Storuman in southern Lapland, merely listings of fossils have been published (Kulling 1942, 1955). Except for the *Eccaparadoxides insularis* Zone, all zones of the *A. oelandicus*, *P. paradoxissimus* and *P. forchhammeri* superzones are present, although never together at one and the same locality. North of Lake Storuman, the Blaik Nappe Complex peters out and the thin autochthonous strata are directly overlain by the Middle Allochthon, with the exception of minor, discontinuous occurrences of Lower Allochthon, e.g. at Storvindeln, in the Gautojaure Window near Adolfström (Kautsky 1940) and at Lake Hornavan. However, north of Kyrkberget at Lake Storuman, Miaolingian fossils have not been found so far, neither in the Autochthon, nor in the Lower Allochthon, with the exception of a few poorly preserved paradoxidid trilobite fragments at one locality near Adolfström (Kulling 1982). This general absence of fossils likely reflects that the Alum Shale does not contain any fossil-preserving limestone concretions (Martinsson 1974; Cederström *et al.* 2012).

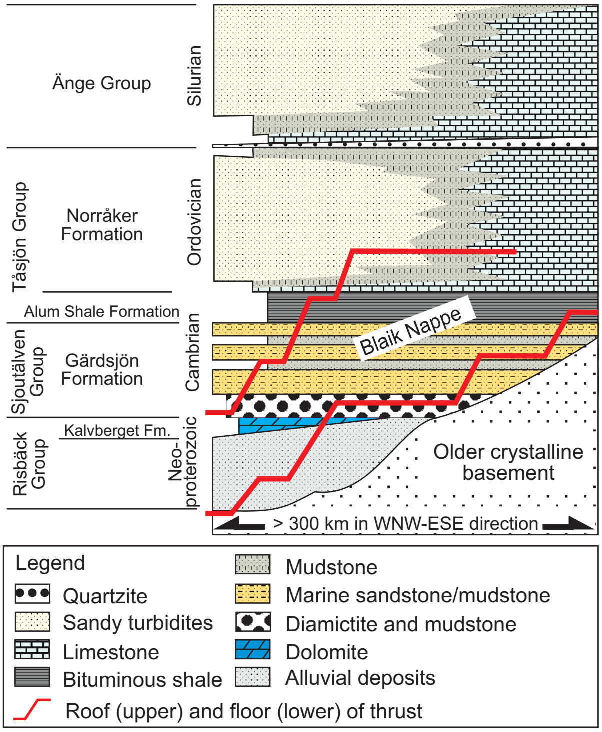


Fig. 5. Stratigraphic column demonstrating the extent of the sedimentary succession in the Blaik Nappe Complex. Modified from Kumpulainen (in Kumpulainen & Greiling 2011) and Greiling *et al.* (2018).

New studies of the Lower Allochthon

Since 2001, Miaolingian trilobites and agnostoids (here treated as a group that is distinct from trilobites) have been sampled by us from the Lower Allochthon at previously known as well as new localities in the Caledonian mountain range in Sweden (Fig. 1). Studied areas include northern Jämtland, the Tåsjö Mountain in Ångermanland, localities between Ormsjön and Storjuktan in the larger Vilhelmina and Storuman areas (southern Lapland), Storvindeln (southern Lapland), the Gautojaure Window (northern Lapland) and Lake Hornavan (northern Lapland) (Fig. 4A, B). The studied localities and collected trilobites and agnostoids are listed in Tables 1 and 2.

Identification of localities was aided by the descriptions published by Asklund & Thorslund (1935) and Asklund (1938) for northern Jämtland and Ångermanland and for Lapland by the geological bedrock maps of the Swedish Geological Survey, Uppsala (SGU, series Ai). Additional unpublished information on localities was received from Reinhard Greiling, Karlsruhe, Germany, who was involved in compiling maps of the studied areas for SGU. In contrast to the autochthonous succession, the Alum Shale in the Lower Allochthon is crushed, folded and faulted and variably overprinted by metamorphism (Fig. 6). Trilobites and agnostoids are often tectonically deformed and found only as disarticulated, more or less fragmentary sclerites. The bituminous limestone concretions and beds within the shale are generally fossiliferous while the shale itself is devoid of fossils. Nodule formation is an early diagenetical

Table 1. Listing of the localities mentioned in the text. The reference coordinate system used is WGS 84.

Northern Jämtland and Tåsjö Mountain area (Ångermanland)			
1	Vedjeön	°Lake section	64°3’45.0“N, 15°22’27.9”E
2	Hillsand	Westergård (1946)	64°6’50.1“N 15°18’51.4”E
3	Havsnäs	°River section	64°10’31.2“N, 15°39’37.6”E
4	Siljeåsen	°Lake section	64°14’1.8“N, 15°35’13.9”E
5	Fånån	°Loose boulder near gravel pit	64°21’18.2“N, 15°19’21.1”E
6	Abborrfallet	*River section	64°25’51.4“N, 15°32’8.0”E
7	Tjärnmyr Mountain	Westergård (1946)	64°27’57.6“N 15°30’55.4”E
8	Högnäsån	*River section	64°23’28.1“N, 15°40’47.7”E
9	Karbäcken	*River section	64°18’54.9“N, 15°46’41.0”E
10	Brattbäcken	°River section	64°17’22.8“N, 15°49’52.9”E
11a	Kvarnbäcken A	*River section	64°15’17.9“N, 15°52’43.4”E
11b	Kvarnbäcken B	*Gravel pit	64°14’25.7“N, 15°51’46.2”E
12	Tåsjö church	*Road profile	64°13’23.7“N, 15°54’39.9”E
13	Sågbäcken	*River section	64°11’46.6“N, 16°0’25.8”E
14	Bellviks Hällan	*Boulders from drainage ditch	64°13’12.9“N, 16°3’6.3”E
15	Rökbergsbäcken	*River section	64°15’36.9“N, 16°0’17.0”E
16	Marbäcken	*River section	64°19’28.2“N, 16°0’53.5”E
Larger Vilhelmina and Storuman areas of southern Lapland (Västerbotten)			
17	Långseleån	*River section near Bredsele	64°31’41.5“N, 15°53’50.9”E
18	Dantas Mountain near Bredsele	°Loose roadside boulders	64°31’36.2“N, 15°55’13.8”E
19	Fjällbränna	*River sections	64°30’37.4“N, 16°0’55.2”E
20	Djupdalsbäcken	*River sections	64°31’50.7“N, 16°20’0.9”E
21a	Stendalsbäcken A	*Upper river section	64°32’18.9“N, 16°22’13.1”E (Fig. #7)
21b	Stendalsbäcken B	*Lower river section	64°32’37.1“N, 16°18’39.0”E
22	Skansholm	°Lake section	64°41’31.5“N, 16°17’1.1”E
23	Granhöjden	Kulling (1955) citing earlier reports	64°47’50.0“N 16°5’18.6”E
24	Strömnäs	*Abandoned Alum Shale quarry	64°47’56.3“N, 16°4’9.8”E
25	Strömnäs	*Lake sections	64°48’12.1“N, 16°4’57.8”E
26	Stalon	°Loose roadside boulders	64°56’25.9“N, 15°48’27.6”E
27	Dorris	Outcrops in road profile	64°59’19.9“N, 15°49’21.3”E – no limestones
28	Ensamheten	River section	65°0’29.9“N, 15°50’41.8”E – no limestones
29	V. Nästansjö	°Loose roadside boulders	64°49’59.8“N, 16°25’51.6”E – no trilobites
30	Ängesbäcken	Kulling (1955) citing earlier reports	
31	Björnbäcken	*River section	64°47’54.7“N, 16°36’46.2”E
32	Granberget Mountain	*Outcrops in road profile	64°49’14.7“N, 16°35’10.6”E
33	Skikkisjö Mountain	Kulling (1955) citing earlier reports	
34	Lubbträsk area	Kulling (1955) citing earlier reports	
35	Långvattnet	*Outcrops in road profile	65°5’19.5“N, 16°39’42.9”E
Storvindeln in southern Lapland (Västerbotten)			
36	Jillesnåle	*Mountain outcrop	65°49’24.6“N, 16°49’33.4”E – no trilobites
37	Hemfjäll	*Road profiles	65°48’28.2“N, 16°53’57.6”E – no trilobites
38	Hemfjäll	*River section	65°48’29.0“N, 16°51’46.2”E
39	Vännäs	*Mountain outcrops	65°48’52.4“N, 16°55’6.5”E – no trilobites (Fig. #8)
40	Yttersberget	*River section	65°46’33.0“N, 17°5’41.2”E – no trilobites
41	Sundraningen	*River section	65°53’46.0“N, 17°4’36.4”E – no limestones
Gautojaure Window in northern Lapland (Norrbotten)			
42	Gaskajaure	*Mountain outcrop	66°16’6.4“N, 16°39’45.9”E – no limestones
43	Viejenäs	*Road profile	66°14’46.4“N, 16°50’18.4”E (Fig. #9)
44	Märkberget	*Mountain outcrop	66°14’0.1“N, 16°51’59.6”E – no limestones
45	Långsjön	*Road profile	66°15’1.2“N, 16°54’10.3”E – no limestones
Lake Hornavan in northern Lapland (Norrbotten)			
46	Bredviken bay:	*Lake section	66°21’54.4“N, 17°10’12.3”E – no trilobites

* = bedrock collecting, ° = loose material.
The reference coordinate system used is WGS 84.

Table 2. Chart showing records of agnostoid and trilobite species at the various collecting sites in the study area. The locality numbers refer to the sites listed in Table 1.

Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**
Agnostus pisiformis				x									x							x		x																								
Homagnostus pater																						x																								
Acidusus aculeatus				x	x	x		x									x		x																											
Acidusus atavus																																														
Goniagnostus nathorsti				x		x		x		x		x	x						x			x											x													
Lejopyge calva						x													x						x																					
Lejopyge elegans																									x							x														
Lejopyge laevigata				x	x	x										x	x		x							G																				
Lejopyge lundgreni											x								x						x																					
Onymagnostus hybridus								x											x													x														
Pentagnostus praecurrens															x	x					x																	x								
Ptychagnostus affinis					x	x		x	x		x			x						x					x							x														
Tomagnostus perrugatus								x																																						
Triplagnostus gibbus						x							x				x						x	x	x								x	x												
Cotalagnostus claudicans																																x														
Cotalagnostus confusus								x									x		x																											
Cotalagnostus greilingi n. sp.																						x																								
Hypagnostus brevifrons	x			x		x		x	x							x			x																											
Hypagnostus lingula						x													x						x							x														
Hypagnostus mammillatus																			x	x												x														
Hypagnostus parvifrons						x		x			x	x		x				x	x	x	x	x								x		x	x	x												
Hypagnostus truncatus				x			x	x						x											x							x														
Tomagnostella exsculpta				x					x	x		x							x			x																								
Doryagnostus incertus						x			x		x										x				x							x	x													
'Diplorrhina' cylindrica																					x																									
'Diplorrhina' depressa																			x																											
'Diplorrhina' quadrata	x					x			x										x																											
Acadagnostus acadicus								x				x		x	x	x	x		x	x		x												x												
Acadagnostus ferox						x			x				x				x		x			x			x	x						x														
Acadagnostus minor	x					x																																								
Acadagnostus spiniger																																x														
Diplagnostus planicauda bilobatus						x	x		x				x					x	x			x			x	x																				
Linguagnostus kjerulfi	x				x			x									x		x																											
Lisogoragnostus confluentus						x																																								
Glaberagnostus bituberculatus				x		x																																								
Glaberagnostus? cicer				x		x													x																											
Megagnostus glandiformis	x					x		x											x																											
Valenagnostus marginatus	x	x		x		x			x	x									x		x	x								x				x												
Eodiscus borealis	x																																													
Eodiscus punctatus				x		x																																								
Proampyx difformis						x		x																																						
Proampyx aculeatus				x		x																																								
Proampyx acuminatus	x				x	x		x											x																											
Proampyx anceps	x																		x																											
Groenwallia microphthalma	x			x		x																																								
Conokephalina ornata						x																																								
Acadoparadoxides torelli											x				x	x					x										x															
Acadoparadoxides oelandicus														x																																
Acadoparadoxides sp.											x				x																							x								
Hydrocephalus vikensis											x				x																															
Paradoxides forchhammeri						x				x			x								x																						x			
Paradoxides paradoxissimus						x			x		x		x	x					x	x	x											x														
Solenopleura? brachymetopa	x	x		x		x			x	x									x																											
Parasolenopleura linnarssoni	x					x		x	x				x																					x												
Kootenia sp.																									x																					
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46

The locality numbers refer to the sites listed in Table 1.

Fig. 6. Tectonized Alum Shale at Marbäcken on the Tåsjö Mountain (locality 16). The exposure is about 2.50 m high. Photo by T. Weidner.

Fig. 7. Large limestone lenses, about 75 cm in diameter, of the *Paradoxides forchhammeri* Superzone in the creek bed at Stendalsbäcken in the Vilhelmina area (locality 21a). Photo by T. Weidner.

process, which favoured localized preservation of the embedded fossil assemblages (Buchardt *et al.* 1997; Bojanowski *et al.* 2019). We have observed that limestone, still abundant on the Tåsjö Mountain and in the Vilhelmina area, become very rare further north (Fig. 7). It is uncertain why this is so but, as a consequence, fossils are extremely rare. Besides, agnostoids and trilobites in the few concretions found, tend to be poorly preserved.

Until recently, the existence of an allochthon sequence at Storvindeln, comprising the 'lower' Cambrian Gärdsjö Formation and the younger Alum Shale Formation, had not been recognized (Kulling 1942; Moczydłowska *et al.* 2001, fig. 1). However, the Alum Shale Formation is accessible in a nearly 300 m continuous outcrop along the shore of Lake Storvindeln and in the mountain north of it in a 100 m long creek ravine (localities nos 38 and 40 in Table 1; for location, see Fig. 4B). There are also several smaller occurrences, most of them in the steep mountain cliffs on the northern side of Lake Storvindeln where the thrust contact between the Alum Shale Formation and the overlying quartzites of the Stalon Nappe is occasionally exposed (Fig. 8). Only one of 24 collected limestones yielded fossil remains. Several blocks were investigated for microfossils, of which two contained lower Tremadocian taxa.

Fig. 8. Exposure at Vännäs near Hemfjäll at Storvindeln (locality 39). A massive meta-arkose of the Stalon Nappe (Middle Allochthon), mylonitic in the basal shear zone, rests on crushed and weathered Alum Shale of the Blaik Nappe Complex (Lower Allochthon). The Middle Allochthon meta-arkose is of Neoproterozoic age and equivalent to the Risbäck Group (see Fig. 5). Photo by T. Weidner. The shown outcrop is about 2 m wide.

Localities are also present in the Lower Allochthon Gautojaure Window (Kautsky 1940) (localities nos 42–45 in Table 1; for location, see Fig. 4B) although outcrops of Alum Shale are extremely rare and generally only loose material was found. The Viejenäs road profile shows about 1–2 m of Alum Shale, vertically squeezed between rocks of the 'lower' Cambrian Gärdsjö Formation, and from a thin limestone layer it yielded fragmentary trilobites (Fig. 9). Several limestone slabs from a different horizon did not contain trilobites.

Fig. 9. An about 6 m high road cutting at Viejenäs (locality 43) in the Gautojaure Window close to Adolfström, showing thin Alum Shale and limestone layers sandwiched between sediments of the Gärdsjön Formation (see Fig. 5). From here originate the fragments of *Paradoxides forchhammeri* illustrated in Figure 50I, J as the northernmost Miaolingian trilobite found in Sweden. Photo by T. Weidner.

Another Lower Allochthon window is exposed at Lake Hornavan in northern Lapland (Norrbotten) (Fig. 4B). In order to locate outcrops, we used Fjällkartan BD16 from Lantmäteriet, unpublished field notes of M. Nordgren (1982, Jäkkvikområdet), the bedrock map of Kulling (1982) and personal information received from Reinhard Greiling, Karlsruhe, Germany. Access to potential localities along the shore between Jäkkvik and Högheden is severely hampered by the lack of roads or trails. One lake section, Bredviken, at low water level showed well-exposed Alum Shale with large but unfossiliferous limestone concretions. The lithology of the limestone is strongly reminiscent of the *P. forchhammeri* Superzone in the Vilhelmina area.

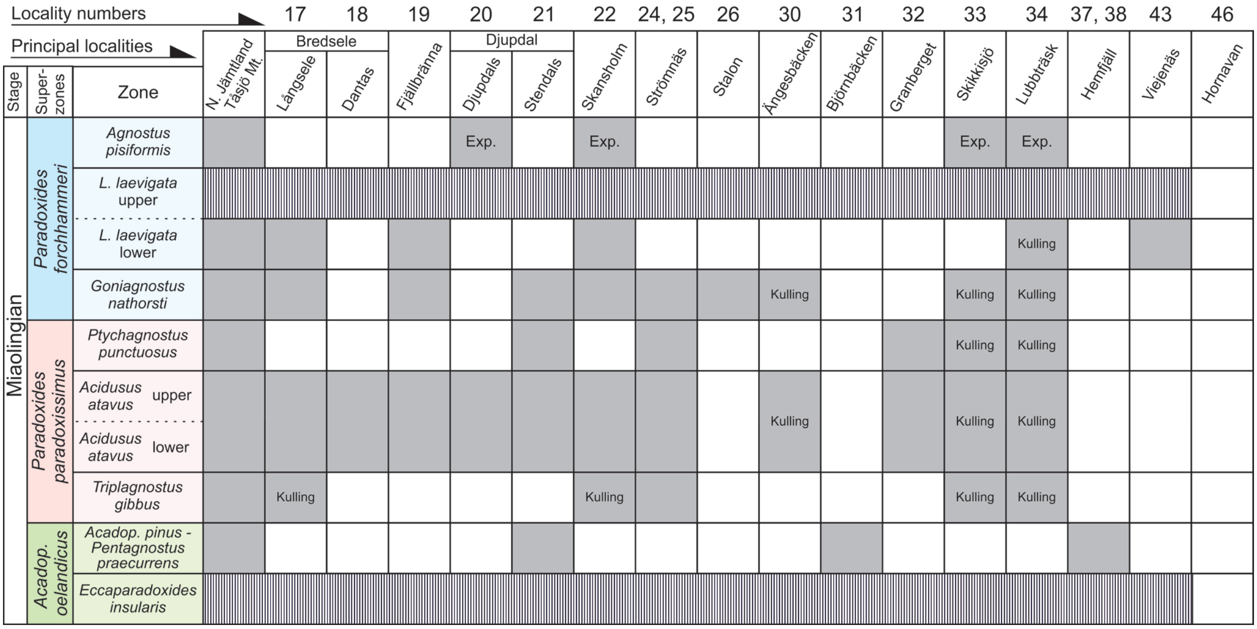
Miaolingian biostratigraphy in Scandinavia

The Miaolingian of Scandinavia is generally highly fossiliferous and a detailed bio- and chronozonation has been established. For several decades, the monographic work of Westergård (1946) served as the standard reference for all work on this interval, but a number of changes have now been introduced. However, a thorough revision with formal definition of type sections and rigorous zonal definitions, like that introduced for the Furongian (Terfelt *et al.* 2008; Nielsen *et al.* 2020), is pending.

The formal definition of the Miaolingian Series replacing the traditional 'Middle' Cambrian in Scandinavia has moved the lower boundary down to include the Kibartian Stage (Nielsen & Ahlberg 2019), which previously was classified as 'lower' Cambrian in Scandinavia (Nielsen & Schovsbo 2011). Only a few, and mostly fragmentary, trilobite remains have been recorded from the Kibartian in Baltoscandia (see summary by Nielsen & Schovsbo 2011). A thorough revision of the sparse fauna is needed before establishing a zonation and here we consider the interval as unzoned in terms of trilobite stratigraphy.

The overlying Bödan Stage comprises, where it is most complete, a lower non-trilobitic interval overlain by strata assigned to the *Acadoparadoxides oelandicus* Superzone, which is subdivided into the *Eccaparadoxides insularis* and *Acadoparadoxides pinus* trilobite zones (see Westergård 1936; Nielsen & Schovsbo 2015). The latter is equivalent to the *Pentagnostus praecurrens* agnostoid Zone and henceforth we use the combined designation *A. pinus* – *P. praecurrens* Zone as proposed by Nielsen & Schovsbo (2015). The non-trilobitic lower part of the Bödan Stage – except for a few taxa appearing immediately below the FAD of *E. insularis* (Westergård, 1936) in drill-cores (see Westergård 1936, pp. 10, 15) – is customarily included in the *E. insularis* Zone, but is here left unassigned. We note that this interval is thicker than the overlying strata containing *E. insularis* in Oelandian drill-cores (Westergård 1936; Hessland 1955). This non-trilobitic interval and the *E. insularis* Zone are currently documented only from Öland (Westergård 1936) and the subsurface of Gotland (Nielsen & Schovsbo 2015) whereas the overlying *A. pinus* – *P. praecurrens* Zone is fairly widely distributed in Scandinavia (Nielsen &

Schovsbo 2015 and references therein). This zone is in turn overlain by sediments of the Almbackenian Stage, comprising the *Paradoxides paradoxissimus* Superzone, which is subdivided in ascending order into the *Triplagnostus gibbus*, *Acidusus atavus* and *Ptychagnostus punctuosus* zones. The *T. gibbus* Zone was informally subdivided into a lower *Paradoxides jemtlandicus* subzone and an upper *Bailiaspis dalmani* subzone by Nielsen & Schovsbo (2015). Informal lower and upper 'parts' (in reality subzones) are also recognized in the *Acidusus atavus* Zone, broadly corresponding to the *Tomagnostus fissus – Ptychagnostus* [here: *Acidusus*] *atavus* and *Hypagnostus parvifrons* zones of Westergård (1946), whereas no subdivision of the *P. punctuosus* Zone has been proposed. The latter zone is overlain by the *Goniagnostus nathorsti* Zone, allocated to the *Paradoxides forchhammeri* Superzone, despite *P. forchhammeri* Angelin, 1851 itself having its First Apparance Datum (FAD) within this zone (probably in the upper part) and not at the base (cf. Brøgger 1878; Høyberget & Bruton 2008, fig. 5). No stage designation has been proposed for the upper part of the Miaolingian in Scandinavia; the stages defined for the Miaolingian of Eastern Europe are not applicable in this region (cf. Nielsen & Schovsbo 2015; Nielsen & Ahlberg 2019). The *G. nathorsti* Zone is in turn followed by the *Lejopyge laevigata* Zone, which is also informally subdivided into a lower and an upper 'part' corresponding to the traditional *Solenopleura*? *brachymetopa* and *L. laevigata* zones, respectively. *Lejopyge laevigata* (Dalman, 1828) has been reported from below the Andrarum Limestone Bed (the traditional *S.*? *brachymetopa* Zone) at Andrarum in SE Scania (Tullberg 1880; Axheimer *et al*. 2006; Ahlberg *et al*. 2009). *Lejopyge laevigata* was also indicated to range from low in the Krekling section in Norway below levels with species characteristic of the '*Solenopleura*? *brachymetopa* Zone' (cf. Brøgger 1878). However, we strongly suspect that these early specimens in Scania and southern Norway in fact represent *Lejopyge calva* Robison, 1964 (see also Høyberget & Bruton 2008). If not, the lower boundary of the *L. laevigata* Zone should be moved down to include the upper part of the traditional *Lejopyge lundgreni – G. nathorsti* Zone *sensu* Westergård (1946). The uppermost part of the Miaolingian is assigned to the *Agnostus pisiformis* Zone. The eponymous species appears in the underlying *L. laevigata* Zone (Westergård 1946) and the lower boundary is defined by the LAD of *L. laevigata* in order to align with the traditional concept of the zone (Axheimer *et al.* 2006; Nielsen *et al.* 2020). The current zonation of the Miaolingian in Scandinavia is shown in Figure 2. With the exception of the *Eccaparadoxides insularis* and the upper part of the *L. laevigata* zones, all of the Miaolingian zones are developed in the study area, but never all at one locality. Lack of natural or man-made outcrops and difficult accessibility in the mountain area as well as the omnipresent tectonic disturbance of the sequence hampered stratigraphical sampling. The zones are discussed below in stratigraphical order (Fig. 10).



Locality numbers				17	18	19	20	21	22	24, 25	26	30	31	32	33	34	37, 38	43	46
Principal localities				Bredsele			Djupdal												
Stage	Super-zones	Zone	N. Jämtland Tåsjö Mt.	Långsele	Dantas	Fjällbränna	Djupdals	Stendals	Skansholm	Strömnäs	Stalon	Ängesbäcken	Björnbäcken	Granberget	Skikkisjö	Lubbträsk	Hemfjäll	Viejenäs	Hornavan
Miaolingian	*Paradoxides forchhammeri*	*Agnostus pisiformis*	■				■ Exp.		■ Exp.						■ Exp.	■ Exp.			
		L. laevigata upper	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	
		L. laevigata lower	■	■		■			■							■ Kulling		■	
		Goniagnostus nathorsti	■	■		■		■	■	■	■	■ Kulling			■ Kulling	■ Kulling			
	Paradoxides paradoxissimus	*Ptychagnostus punctuosus*	■					■		■				■	■ Kulling	■ Kulling			
		Acidusus atavus upper	■	■	■	■	■	■	■	■		■ Kulling		■	■ Kulling	■ Kulling			
		Acidusus atavus lower	■	■	■	■	■	■	■	■		■		■	■	■			
		Triplagnostus gibbus	■	■ Kulling					■ Kulling	■					■ Kulling	■ Kulling			
	Acadop. oelandicus	*Acadop. pinus - Pentagnostus praecurrens*	■					■					■				■		
		Eccaparadoxides insularis	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	▥	

Fig. 10. Distribution chart showing the occurrence of biozones at the principal fossiliferous localities in Väster- and Norrbotten. For locality numbers: see Table 1. The lower part of the Miaolingian up to and including the *E. insularis* Zone and the upper part of the *L. laevigata* Zone (vertically shaded) were not encountered. Trilobite occurrences in Kulling (1955) are a review of finds made by early pioneers in the area. For northern Jämtland and the Tåsjö Mountain, localities 1 to 16 are combined into one column. Lower and upper parts of the *T. gibbus* Zone cannot be recognized due to the general lack of trilobites. 'Exp.' = Exporrecta Conglomerate Bed.

All references are to the Lower Allochthon unless otherwise stated. Ranges of the discussed species as well as all other taxa described from Scandinavia are listed in Appendix 2.

Unzoned interval

No Kibartian strata have been identified in the Caledonides so far, where this interval forms part of the extensive Hawke Bay hiatus (Nielsen & Schovsbo 2015). This hiatus also includes the unzoned basal part of the Bödan Stage as well as the *E. insularis* Zone (see below).

Eccaparadoxides insularis Zone

Fossils characteristic of this zone have not been found in the study area. From the autochthon of southern Jämtland, Westergård (1946) reported finding *Condylopyge regia* (Sjögren, 1872), which he took to indicate the possible presence of the *E. insularis* Zone (compare Westergård 1936). Karis (1998, p. 66) also suggested the presence of this zone in the area of Berg (villages Skucku and Bingsta). The fossil record was not documented, but likely also referred to finding *C. regia*, which is common in the autochthon in the area but in association with trilobites characteristic of the *A. pinus – P. praecurrens* Zone (Rushton & Weidner 2007). We have encountered no fossil evidence demonstrating the presence of the *E. insularis* Zone in the autochthon or the allochthon.

Acadoparadoxides pinus–Pentagnostus praecurrens Zone

This zone has been documented in the allochthonous strata exposed at Kvarnbäcken, Bellviks Hällan, Rökbergsbäcken and Marbäcken on the Tåsjö Mountain, at Stendalsbäcken near Djupdal and Björnbäcken in the Vilhelmina area, and at the shore of Storvindeln near Hemfjäll. *Pentagnostus praecurrens* (Westergård, 1936) itself is common in samples collected at Rökbergsbäcken and Marbäcken and at Stendalsbäcken and Storvindeln. Both occurrences represent the *A. pinus–P. praecurrens* Zone, but it should be noted that rare specimens of *P. praecurrens* have been recorded from the overlying *T. gibbus* Zone in southernmost Sweden (Weidner & Nielsen 2014). Fairly abundant material of *Acadoparadoxides torelli* (Westergård *in* Asklund & Thorslund, 1935), another species characteristic of the *A. pinus – P. praecurrens* Zone, was collected at Kvarnbäcken, Rökbergsbäcken, Marbäcken, Stendalsbäcken and Björnbäcken. *Acadoparadoxides oelandicus* (Sjögren, 1872) was recorded by Weidner *et al.* (2014) from Bellviks Hällan, but based on only one pygidium. A couple of unassignable cranidia, here treated as *Acadoparadoxides* sp., have been collected from the *A. pinus–P. praecurrens* Zone at Kvarnbäcken and Rökbergsbäcken (Weidner *et al.* 2014) and at Hemfjäll. *Hydrocephalus vikensis* Rushton & Weidner, 2007 and *Acadagnostus acadicus* (Hartt *in* Dawson, 1868) were also recorded from the *A. pinus–P. praecurrens* Zone at Kvarnbäcken and Rökbergsbäcken, respectively, by Weidner *et al.* (2014) and these authors also found extensive material of *Hydrocephalus* sp. at the latter locality. No additional material of these species has been found during the present study. Kulling (1955) reported *A. acadicus* from Marbäcken and Thorslund (1949) described *Kootenia westergaardi* Thorslund from the *A. pinus–P. praecurrens* Zone of the Skute nappe, south of Brunflo in southern Jämtland (i.e. outside our study area). No additional material of this very rare species has been found during the present study (for remarks on *Kootenia* sp., see the *A. atavus* Zone).

Triplagnostus gibbus Zone

The eponymous species is quite abundant, albeit poorly preserved, in samples collected at Strömnäs. Rare specimens have been found also at Abborrfallet in northern Jämtland and at Sågbäcken on the Tåsjö Mountain. The species occurs alone or is associated with *A. acadicus* (see also Kulling 1955); no other associated fauna has been recorded and the assemblage is of unusually low diversity. Kulling (1955) also recorded *T. gibbus* (Linnarsson, 1869) from Långseleån, Granhöjden near Strömnäs, Skikkisjö Mountain and Lubbträsk in the Vilhelmina and Storuman areas, so the zone seems to be fairly widespread in the Lower Allochthon. It is impossible to distinguish subzones. From the far south of our study area, at Vedjeön, Westergård (1950, 1953) reported *Eodiscus borealis* Westergård, 1946, *Ctenocephalus exsulans* (Linnarsson, 1879), *Solenopleura*? *parva* Linnarsson, 1879 and *Parasolenopleura aculeata* (Angelin, 1851) from boulders, all taxa distinctive of the *T. gibbus* Zone. Asklund & Thorslund (1935) and Asklund (1938) treated a limestone layer with *Conocoryphe* cf. *C. impressa* [now: *Bailiella impressa* (Linnarsson, 1879)] at Fånån, also in the southern part of the study area, as an equivalent to the Exsulans Limestone Bed of Scania. We have not observed equivalents of this bed in the study area.

Acidusus atavus Zone

It is not possible to differentiate between the lower and upper parts of this zone as in Scania in southern Sweden and on Bornholm, Denmark, because taxa characteristic of the lower part are entirely lacking, above all *Tomagnostus fissus* (Lundgren *in* Linnarsson, 1879). Strata assignable to the *A. atavus* Zone are the most common in the Miaolingian of the Lower Allochthon and have been encountered at Fånån and Abborrfallet in northern Jämtland, at Högnäsån, Karbäcken, Brattbäcken, Kvarnbäcken, Tåsjö church as well as Bellviks Hällan on the Tåsjö Mountain, and at Långseleån, Dantas Mountain, Fjällbränna, Djupdalsbäcken, Stendalsbäcken, Skansholm, Strömnäs and Granberget in the larger Vilhelmina area. To these may be added Marbäcken, Ängesbäcken, the Skikkisjö Mountain and Lubbträsk (Kulling 1955). *Acidusus atavus* (Tullberg, 1880) itself has been found abundantly at Högnäsån, Tåsjö church, Långseleån, Fjällbränna and Djupdalsbäcken, and one specimen was found at Karbäcken. Very common *Hypagnostus lingula* (Grönwall, 1902) has been recorded at Fjällbränna, Strömnäs and Granberget. Asklund & Thorslund (1935) also reported it from Abborrfallet. Other common species in the zone are *Onymagnostus hybridus* (Brøgger, 1878) (Högnäsån, Fjällbränna and Granberget), *Ptychagnostus affinis* (Brøgger, 1878) (Fånån, Abborrfallet, Högnäsån, Karbäcken, Kvarnbäcken, Bellviks Hällan, Djupdalsbäcken, Strömnäs and Granberget), *Hypagnostus mammillatus* (Brøgger, 1878) (Fjällbränna, Djupdalsbäcken and Granberget), *Hypagnostus parvifrons* (Linnarsson, 1869) (Abborrfallet, Högnäsån, Kvarnbäcken, Tåsjö church, Bellviks Hällan, Dantas Mountain, Fjällbränna, Djupdalsbäcken, Stendalsbäcken, Skansholm, Ängesbäcken, Granberget, Skikkisjö Mountain and Lubbträsk) and *Acadagnostus acadicus* (Högnäsån, Tåsjö church, Bellviks Hällan, Fjällbränna and Djupdalsbäcken). The latter species has a long range and is of little biostratigraphic significance (see Systematics). Within the study area, Weidner *et al.* (2014) reported it from the *A. pinus – P. praecurrens* Zone at Rökbergsbäcken and Kulling (1955) listed it from the *T. gibbus* Zone at Långseleån, Skansholm and Lubbträsk.

In addition to these common species, several rarer taxa have also been found in the *A. atavus* Zone, viz. *Tomagnostus perrugatus* (Grönwall, 1902) (Högnäsån), *Cotalagnostus claudicans* Westergård, 1946 (Granberget), *Hypagnostus clipeus* Whitehouse, 1939 (Granberget), *Hypagnostus truncatus* (Brøgger, 1878) (Högnäsån, Bellviks Hällan and Granberget; also listed from Siljeåsen and the Tjärnmyr Mountain by Westergård 1946), '*Diplorrhina*' *depressa* (Westergård, 1946) (Fjällbränna), *Diplagnostus planicauda bilobatus* Kobayashi, 1939 (Abborrfallet, Dantas Mountain, Fjällbränna, Strömnäs) and *Doryagnostus deltoides* Robinson, 1978 (Granberget). All of these species are known from the *A. atavus* Zone elsewhere in Scandinavia and/or from ice-rafted boulders in northern Germany but several are not confined to this stratigraphic level (for details, see Appendix 2 and Systematics).

Very few species of trilobites have been recorded in the zone. *Paradoxides paradoxissimus* (Wahlenberg, 1818) was found at Karbäcken, Bellviks Hällan, Fjällbränna, Djupdalsbäcken and Stendalsbäcken. Small fragments, almost certainly representing this species, have been recorded at several other localities (Asklund & Thorslund 1935). This long-ranging species is of limited biostratigraphic value. A fragment-limestone bed at Stendalsbäcken yielded unusually large cranidia of this species, up to five cm long. *Parasolenopleura linnarssoni* (Brøgger, 1878), collected at Högnäsån and Karbäcken on the Tåsjö Mountain, are occasional finds. The species is reported previously also from Abborrfallet (Asklund & Thorslund 1935), Vedjeön and Sågbäcken (Westergård 1953) and Lubbträsk (Kulling 1955). It is known mainly from the *A. atavus* Zone, but it also occurs rarely in the overlying *P. punctuosus* Zone elsewhere in Scandinavia (see Systematics for details). A single pygidium of the 'exotic' taxon *Kootenia* sp. has been collected at Strömnäs.

Ptychagnostus punctuosus Zone

This zone is here documented from Abborrfallet in northern Jämtland, Karbäcken and Kvarnbäcken on the Tåsjö Mountain and Stendalsbäcken, Strömnäs and Granberget in the Vihelmina and Storuman areas; Kulling (1955) reported it from the Skikkisjö Mountain. The eponymous species has not been recorded in the present study, but Westergård (1946) listed it from Hillsand and the Tjärnmyr Mountain. *Lejopyge elegans* (Tullberg, 1880) is an infrequent species known only from the *P. punctuosus* Zone in Scandinavia; in the study area it has been recorded at Strömnäs and Granberget. *Doryagnostus incertus* (Brøgger, 1878), another generally infrequent species known almost exclusively from the *P. punctuosus* Zone elsewhere in Scandinavia, has been found at Abborrfallet, Karbäcken, Kvarnbäcken, Stendalsbäcken, Strömnäs, Granberget and it was mentioned from the Skikkisjö Mountain by Kulling (1955). Sparse material of the rare trilobite *Conokephalina ornata* (Brøgger, 1878) was found in the *P. punctuosus* Zone at Abborrfallet; elsewhere in Scandinavia it known from this zone and the overlying *G. nathorsti* Zone (see Systematics).

All other species found at this level are not zone-specific. *Lejopyge lundgreni* (Tullberg, 1880) was collected from this zone at Kvarnbäcken and Strömnäs and also from the overlying *G. nathorsti* Zone at the latter locality. Elsewhere in Scandinavia, this species is most common in the *G. nathorsti* Zone, but ranges from the uppermost part of the *P. punctuosus* Zone (Westergård 1946). *Acadagnostus ferox* (Tullberg, 1880), which also is long-ranging, was found in the *P. punctuosus* Zone at Abborrfallet, Granhöjden, Strömnäs and Granberget. A few specimens of *Hypagnostus truncatus* were collected from the *P. punctuosus* Zone at Strömnäs, but this species is more common in the *A. atavus* Zone in the study area. One cephalon of an as yet undescribed '*Diplorrhina*' species was found in the *P. punctuosus* Zone at Stendalsbäcken. In Scandinavia, representatives of this genus range through the *A. atavus*, *P. punctuosus* and lower part of the *L. laevigata* zones. '*Diplagnostus*' *planicauda bilobatus* was reported from the *P. punctuosus* Zone and the *P. forchhammeri* Superzone at several localities in northern Jämtland and the Tåsjö Mountain by Westergård (1946). No new material of this species has been collected from the *P. punctuosus* Zone during the present study. This species ranges from the *A. atavus* Zone (Bornholm) to the lowermost part of the *L. laevigata* Zone (southern Sweden) and it thus has limited stratigraphic significance. *Glaberagnostus*? *cicer* (Tullberg, 1880) was found at Abborrfallet together with *D. incertus* and *C. ornata*; it has a known range from the *P. punctuosus* Zone into the lower part of the *L. laevigata* Zone and is also of little stratigraphic significance (see Systematics for details). *Eodiscus punctatus* (Salter, 1864) was found in the *P. punctuosus* Zone at Abborrfallet, but its FAD is in the underlying *A. atavus* Zone elsewhere in Scandinavia (Westergård 1946). The long-ranging *Paradoxides paradoxissimus* was collected from the *P. punctuosus* Zone at Kvarnbäcken, Stendalsbäcken, and Granberget.

Goniagnostus nathorsti Zone

The *G. nathorsti* Zone is defined by the FAD of the eponymous species (Westergård 1946) and also *Tomagnostella exsculpta* (Angelin, 1851) [usually recorded as *T. nepos* (Brøgger, 1878)] appears at this level. However, we note that *G. nathorsti* (Brøgger, 1878) has been reported to occur rarely in the *P. punctuosus* Zone (Rudolph 1994, pp. 66, 67), and TW has also found it in a loose boulder at Gislövhammar, Scania, associated with a similar 'old' assemblage. As these occurrences are based on loose boulders, they are ignored for the time being, but it is possible that the base of the *G. nathorsti* Zone should be defined by the LAD of *P. punctuosus* (Angelin, 1851).

Trilobites are extremely rare in the *G. nathorsti* Zone in Norway (Brøgger 1878; Strand 1929; Høyberget & Bruton 2008) and none have been described from Sweden so far (Westergård 1953). No agnostoids, not even the eponymous species, are confined to this zone, but range from the older *P. punctuosus* Zone or into the lower part of the *L. laevigata* Zone (see Westergård 1946). However, a good indication for the *G. nathorsti* Zone is the mass occurrence of the eponymous species, mostly alone, which is the case at Siljeåsen in northern Jämtland, Sågbäcken on the Tåsjö Mountain and Fjällbränna and Skansholm in the Vilhelmina area. Alternatively, the agnostoid assemblage comprising *G. nathorsti*, *T. exsculpta*, *D. planicauda bilobatus*, *Glaberagnostus*? *cicer* and *Valenagnostus marginatus* (Brøgger, 1878) is taken as characteristic of the zone, providing that these long-ranging taxa are not associated with any of the zone-specific *Hypagnostus brevifrons* (Angelin, 1851), '*Diplorrhina*' *quadrata* (Tullberg, 1880), *Linguagnostus kjerulfi* (Brøgger, 1878), *Glaberagnostus bituberculatus* (Angelin, 1851) or *Groenwallia microphthalma* (Angelin, 1851), all of which are characteristic of the lower part of the *L. laevigata* Zone. At Siljeåsen and Abborrfallet in northern Jämtland, at Sågbäcken on the Tåsjö Mountain and at Långseleån, Fjällbränna, Skansholm and Lubbträsk in the the larger Vilhelmina and Storuman areas, the *G. nathorsti* and *L. laevigata* zones can be separated based on these criteria. At other localities, however, the fossil record is meager and cannot safely be allocated to a distinct zone and may represent the *G. nathorsti* Zone or the lower part of the *L. laevigata* Zone. This is so for the localities Tåsjö church on the Tåsjö Mountain (Asklund & Thorslund 1935), and Stalon, Ängesbäcken and the Skikkisjö Mountain in the larger Vilhelmina and Storuman areas; the last two were cited by Kulling (1955).

Goniagnostus nathorsti is common in the eponymous zone at Siljeåsen, Abborrfallet, Sågbäcken, Fjällbränna and Skansholm and is further reported from the Tåsjö church by Asklund & Thorslund (1935) and from the Skikkisjö Mountain by Kulling (1955). Isolated finds of this species are from Högnäsån and Brattbäcken. Another characteristic species in the *G. nathorsti* Zone is *Lejopyge calva*, which is common at Fjällbränna and Strömnäs and rare at Abborrfallet. This is the first record of this species from Sweden. It was reported from the *G. nathorsti* Zone of southern Norway by Høyberget & Bruton (2008) and we have observed it at the same level on Bornholm (unpublished). *Lejopyge calva* seems to range into the lower part of the *L. laevigata* Zone in the study area (see below). *Lejopyge lundgreni* was collected from the *G. nathorsti* Zone at Fjällbränna and Strömnäs. This species is most common in the *G. nathorsti* Zone but ranges from the uppermost *P. punctuosus* Zone (Westergård 1946), where it also has been found at Strömnäs. *Tomagnostella exsculpta* was found at Brattbäcken, in the banks of the Fjällbränna creek, where it is abundant, and on the coast near Skansholm. Other occurrences are from the lower part of the *L. laevigata* Zone (see below). *Acadagnostus ferox* is common in the *G. nathorsti* Zone at Abborrfallet, Sågbäcken, Långseleån, Fjällbränna, Skansholm, Strömnäs and Stalon. Rare specimens from Karbäcken belong either to this zone or the lower part of the *L. laevigata* Zone. It is a long-ranging species, locally occurring already in the *A. atavus* Zone (see Systematics), and in the study area it has been found in the *P. punctuosus* Zone (see above). *Diplagnostus planicauda bilobatus* is another long-ranging species, which is common in the *G. nathorsti* Zone at Fjällbränna, Skansholm, Strömnäs and Stalon. At Siljeåsen, Abborrfallet and Karbäcken it occurs in samples representing either the *G. nathorsti* Zone or the lower part of the *L. laevigata* Zone. Westergård (1946) reported it as common in the *P. forchhammeri* Superzone at several localities in northern Jämtland (Vedjeön, Hillsand, Tjärnmyr Mountain) and from Sågbäcken on the Tåsjö Mountain. *Valenagnostus marginatus* was found at Fjällbränna and Stendalsbäcken and is mentioned by Kulling (1955) from Skansholm. At other localities it occurs in the lower part of the *L. laevigata* Zone (see below).

At Brattbäcken and Stendalsbäcken, *P. forchhammeri* was collected together with a few specimens of *G. nathorsti*, *T. exsculpta* and the more common *V. marginatus*, and at Skansholm with *G. nathorsti*, *T. exsculpta*, *Diplagnostus planicauda bilobatus* and *Acadagnostus ferox*. These assemblages are characteristic of the *G. nathorsti* Zone.

Lejopyge laevigata Zone: Lower part

Limestone from this level is scarce in the northern part of our study area (Västerbotten) but the characteristic fauna has, nonetheless, been collected at several localities, viz. Långseleån, Fjällbränna and Skansholm, and Kulling (1955) noted an occurrence at Lubbträsk. In the southern part of the study area, the zone is encountered more frequently and fossils are occasionally abundant, i.e. at Vedjeön, Siljeåsen, Fånån and Abborrfallet in northern Jämtland, and at Högnäsån, Karbäcken, Brattbäcken and Marbäcken on the Tåsjö Mountain. Our collections correspond essentially to the faunal assemblage published by Asklund & Thorslund (1935).

Only two pygidia of *L. laevigata* itself have been found, one at Långseleån and one at Fjällbränna; the associated fauna is clearly indicative of the lower part of the eponymous zone. Elsewhere in Scandinavia, this species ranges throughout the *L. laevigata* Zone, being most common in the upper part. Records of *L. laevigata* from Fånån and Abborrfallet (Asklund & Thorslund 1935, pp. 96, 95) also derive from the lower part of the zone, while an unusual assemblage described from Siljeåsen by these authors (Asklund & Thorslund 1935, p. 98), comprising *G. nathorsti*, *P. punctuosus*, *Glaberagnostus*? *cicer* and *L. laevigata*, is suggestive of the *G. nathorsti* Zone, if we assume that '*L. laevigata*' in fact represents *L. calva*. A single find of *L. laevigata* (or *L. calva*?) at Stalon (Gee 1972) is without accompanying fauna, precluding safe identification of biozone. Kulling's (1955) record of *L. laevigata* from Marbäcken on the Tåsjö Mountain and Lubbträsk probably derives from the lower part of the zone, judging from the associated fauna. Several additional species, known only from the lower part of the *L. laevigata* Zone in southern Scandinavia, have been encountered in the study area. Two cephala of *Homagnostus pater* (Westergård *in* Holm & Westergård, 1930) were collected from one block of limestone at Skansholm, associated with sparse material of *Cotalagnostus greilingi* n. sp. An extensive material of *Acidusus aculeatus* (Angelin, 1851) was reported from Siljeåsen, Fånån and Abborrfallet by Asklund & Thorslund (1935), and new material has been collected by us at Högnäsån, Långseleån and Fjällbränna. Sparse and poorly preserved material of *Cotalagnostus confusus* (Westergård *in* Holm & Westergård, 1930) was collected at Högnäsån, Långseleån and Fjällbränna. *Hypagnostus brevifrons* was collected at Vedjeön, Siljeåsen and Abborrfallet, Högnäsån and Fjällbränna, and reported from Marbäcken by Kulling (1955) and from Karbäcken by Asklund & Thorslund (1935); it is quite common at several of these localities. Sparse material of '*Diplorrhina*' *quadrata* was found at Vedjeön, Abborrfallet, Karbäcken and Fjällbränna. Mostly fragmentary material of *Linguagnostus kjerulfi* has been collected at Vedjeön, Högnäsån, Långseleån and Fjällbränna and it was reported from Fånån by Asklund & Thorslund (1935). A single complete specimen of *Lisogoragnostus confluentus* (Rudolph, 1994) was found at Abborrfallet; this is the first record of this species from Sweden. A few specimens of the large agnostoid *Megagnostus glandiformis* (Angelin, 1851) were found at Högnäsån and Långseleån;

Westergård (1946) also reported it from Vedjeön and Abborrfallet. *Glaberagnostus bituberculatus* was found at Siljeåsen and Abborrfallet; it is also recorded from the latter locality by Asklund & Thorslund (1935) and Westergård (1946). The latter species is known from the lower part of the *L. laevigata* Zone in southern Scandinavia but rare occurrences from the upper part of the zone are also recorded (see Systematics). *Glaberagnostus*? *cicer*, found at Siljeåsen, Abborrfallet and Fjällbränna, is a long ranging species of little biostratigraphic value; the associated fauna at these sites is indicative of the lower part of the *L. laevigata* Zone. A smaller but similar fauna was described from Fånån by Asklund & Thorslund (1935, p. 97). Other species, known to range from the *G. nathorsti* Zone, are *Tomagnostella exsculpta*, collected at Siljeåsen and Karbäcken, and *Valenagnostus marginatus*, collected at Siljeåsen, Abborrfallet and Karbäcken; the latter species was reported from Lubbträsk by Kulling (1955). It is not possible to determine the precise zone for the material reported from Vedjeön, Hillsand, Brattbäcken and Ängesbäcken by Kulling (1955) and Westergård (1946). Westergård (1946) reported *Acadagnostus minor* (Brøgger, 1878) from Vedjeön and Abborrfallet; we did not find additional material.

Several trilobites, confined to the lower part of the *L. laevigata* Zone in southern Scandinavia, have been found in the study area. *Groenwallia microphthalma* was collected at Vedjeön and Abborrfallet and reported from Siljeåsen by Westergård (1953). Of *Proampyx*, all four species known from Scandinavia were found: *Proampyx difformis* (Angelin, 1851) at Abborrfallet and Högnäsån; *Proampyx aculeatus* (Angelin, 1851) is recorded from Siljeåsen by Westergård (1953) and it is common in the highly fossiliferous beds at Abborrfallet; *Proampyx acuminatus* (Angelin, 1851) was reported from Vedjeön, Fånån and Abborrfallet by Asklund & Thorslund (1935) and from Högnäsån and Fjällbränna by Westergård (1953), and *Proampyx anceps* Westergård (1953) occurs infrequently at Vedjeön and Fjällbränna. *Solenopleura*? *brachymetopa* (Angelin, 1851) was collected at Vedjeön, Abborrfallet and Fjällbränna. Westergård (1953) recorded it also from Hillsand, Siljeåsen, Brattbäcken and Karbäcken.

Paradoxides forchhammeri has been found at Abborrfallet, where it is associated with various agnostoids characteristic of the lower part of the *L. laevigata* Zone, viz. *H. brevifrons*, *D. quadrata*, *G. bituberculatus*, *M. glandiformis* as well as several trilobites. At Viejenäs, a few fragments were found without associated agnostoids; *P. forchhammeri* has been reported also from Sågbäcken by Asklund & Thorslund (1935). Except for Abborrfallet, *P. forchhammeri* occurs only sporadically in the studied sections. Fragmentary material of *P.* cf. *forchhammeri* was recorded from Fånån, Karbäcken and Kvarnbäcken by Asklund & Thorslund (1935).

Lejopyge laevigata Zone: Upper part

In Scandinavia, the upper part of the *L. laevigata* Zone is characterized by a number of trilobites and agnostoids confined to this level, but none have been found in the study area. However, the general scarcity of limestone nodules, especially at the northern localities, makes it difficult to verify its presence or absence in the Lower Allochthon. The eponymous species is rare and has been found so far only in the lower part of the zone (see above). We note that the upper part of the *L. laevigata* Zone appears to be very thin in the Autochthon and Lower Allochthon in southern Jämtland (Karis 1998) and we suspect that it is entirely absent in the study area (see remarks below on the Exporrecta Conglomerate Bed). This is peculiar, considering that the lower part is developed at a time when the sea level was low; this stratigraphic level is often replaced by the Exporrecta Conglomerate Bed in south-central Sweden (Westergård 1946; Martinsson 1974). Subsequently, the sea level rose significantly and Alum Shale was again deposited across south-central Sweden, but not in the study area. It is likely that the outer shelf represented by the Lower Allochthon was uplifted at this stage.

Exporrecta Conglomerate Bed and *Agnostus pisiformis* Zone

From northern Jämtland and the Tåsjö Mountain, *Agnostus pisiformis* (Wahlenberg, 1818) is reported from Siljeåsen and Sågbäcken (Asklund & Thorslund 1935). In the Vilhelmina area, material of *A. pisiformis* was found in a single loose block on the shore at Skansholm. The block also contained *Oligomys exporrecta* (Linnarssoni, 1876) and seemingly represents the Exporrecta Conglomerate Bed. Westergård (1922, p. 96) also reported *A. pisiformis* from this locality, occurring in bituminous limestone, and Kulling (1955) described a conglomerate (collected by Wiman) with *O. exporrecta* being in contact with bituminous limestone containing *A. pisiformis* (Kulling 1955, p. 149). He further recorded the Exporrecta Conglomerate from Djupdal (Baktoberget), the Skikkisjö Mountain and Lubbträsk, but at these sites no fossils were found during this study. *Agnostus pisiformis* has a range from the upper part of the *L. laevigata* Zone through the eponymous zone; it occurs in the Exporrecta Conglomerate Bed only in areas where the upper part of the *L. laevigata*

Zone is absent (Westergård 1946). No other faunal indications of the *A. pisiformis* Zone have been noted.

Miaolingian biofacies in Scandinavia

Miaolingian fossils have been described from nearly all provinces of Scandinavia, where Palaeozoic strata are preserved, but with the main emphasis being on taxonomy and stratigraphy. Palaeoecological aspects are mentioned only cursorily, if treated at all, and no studies analyse regional differences in faunal composition. Undertaking such an analysis is encumbered by the lack of quantitative datasets on abundance, but alternatively, as a first step, a qualitative approach can be attempted by analysing presence/absence and semi quantitative abundances (common, infrequent, rare etc.). This is the tentative *modus operandi* adopted here, where we focus on the *P. paradoxissimus* – *P. forchhammeri* interval. For a few remarks on the *A. oelandicus* Superzone, see discussion below.

A characteristic property of the Miaolingian assemblages described from all over Scandinavia is the ubiquitous presence of agnostoids (e.g. Westergård 1946; Høyberget & Bruton 2008; Weidner & Nielsen 2014). Discussions on the palaeoecology of agnostoids mostly centre on their mode of living, notably the question whether they were pelagic or benthic; see Fortey & Owens (1999, pp. 455–458) for an exhaustive review of the more or less speculative proposals for agnostoid lifestyle published over the years. Lochman-Balk & Wilson (1958), Robison (1972a, b), Pegel (2000) and Babcock 1994b) have noted that agnostoids were far more common on the outer shelf than in inboard settings.

We here follow Nielsen (1997) who inferred that Cambrian agnostoids were benthic and typical inhabitants of oxygen-reduced environments, whereas many Ordovician representatives seem to have preferred well oxygenated environments (see Pek 1977; Nielsen 1995, 1997, 1999). This interpretation is based on the observation that diversity, abundance and species composition of agnostoid assemblages varies geographically as well as stratigraphically within the Miaolingian–Furongian Alum Shale Formation of Scandinavia (e.g. Westergård 1946; Ahlberg & Terfelt 2012; this study). This is explained most easily by presuming that the agnostoids were benthic and the regional and temporal changes in our interpretation translate into preferences for different depth settings within the basin. The faunal differences seem to have been primarily oxygen controlled, but temperature and availability of nutrients may also have played a role. In support of this inference, we direct attention to the Furongian of Scandinavia, where the lithofacies distribution clearly shows that the sea level overall was lower than in the later part of the Miaolingian. This conclusion is based on the recurrent gaps in the Furongian succession and the common presence of bituminous bioclastic limestones consisting of winnowed olenid trilobites everywhere in south-central Sweden (see Nielsen & Schovsbo 2015 and Nielsen *et al.* 2020). Both features relate to lowering of the storm wave base during recurrent sea-level lowstands. However, despite the overall shallower depositional depth, agnostoids are extremely rare in the Furongian, except for the near monospecific occurrence of *Homagnostus obesus* (Belt, 1867) in the *Olenus* Superzone (Ahlberg & Ahlgren 1996; Ahlberg & Terfelt 2012). If the agnostoids were pelagic, this near absence in the Furongian is counterintuitive, whereas it is entirely consistent with the assumption that the bottom environment was too dysoxic for a benthic lifestyle preventing agnostoid habitation despite deposition in shallower water than in the late Miaolingian. In the Miaolingian, agnostoid diversity decreases in a palaeo-outboard direction in Scandinavia and which is taken as reflecting a declining oxygen level in the bottom environment.

A benthic mode of life does not rule out that some or perhaps even most agnostoids were epibenthic (cf. Pek 1977; Slavíčková 2001), living attached to for instance sponges (spicules are locally common in the Alum Shale, see Castellani *et al.* 2012). Müller & Walossek (1987) inferred from a consideration of the limb morphology that agnostoids lived enrolled, i.e. ostracod-like. Their skeleton was obviously designed for perfect enrolment, so we support this deduction. This would for instance explain the odd forward bend of the distal part of the thoracic segments, which is not a particularly streamlined feature if the agnostoids lived outstretched and should move forwards, regardless of whether they swam or moved on the sea-floor. This morphology is totally different from what is seen in trilobites including eodiscoids. Also, in outstretched position there are gaps between the sclerites in the thoracic region which is an additional strong argument for inferring an enrolled mode of life (Müller & Walossek 1987, fig. 1; see also their discussion pp. 40–42 and figs 16, 25).

We distinguish three benthic biofacies in the *P. paradoxissimus* – *P. forchhammeri* interval of Scandinavia (Figs 11, 12). I) Well-oxygenated primary limestone facies with common trilobites (high diversity) and uncommon agnostoids (low to medium diversity). II) Dysoxic shale facies with some trilobites (moderate diversity) and common agnostoids (high diversity). III) Dysoxic shale facies with rare or no trilobites and common agnostoids (moderate to low diversity). Biofacies II and III grade transitionally into each other and within facies III, the most offshore parts are characterized by very low diversity, and just one or a few agnostoid species dominate at each stratigraphical level. The species composition (both presence/absence and differences in abundance) also varies between the three facies, which concerns both trilobites and agnostoids (see discussion and Appendix 2).

Biofacies I: Well-oxygenated bioclastic limestone facies

Thin beds of bioclastic limestone occur at several levels in the Miaolingian, e.g. the Forsemölla, Exsulans and Andrarum Limestones (all < 1 m thick, mostly some decimetres; see Nielsen & Schovsbo 2007 for review). This type of limestone should not be confused with the bituminous limestone lenses and beds that are common in the Alum Shale Formation (called stinkstone, orsten or anthraconite). The bioclastic limestone beds – that are geographically widespread despite their very limited thickness – seem to have been deposited under well oxygenated conditions, where accumulations of disintegrated shells formed limestone during the early phase of sea-level rises in the aftermath of major sea-level lowstands (see Nielsen & Schovsbo 2011, p. 216 and 2015, pp. 297, 298). The generally fragmentary state of the fossils is indicative of comparatively turbulent water and the facies likely represents an environment above the storm wave base. In comparison with the surrounding shales, trilobites are common in the limestones although the sclerites are usually intensively fragmented, and many species are described from the Exsulans and Andrarum Limestones (Fig. 11; see also Appendix 2). It is a common trait of these limestones that agnostoids are present, but infrequently so, although quite a few species are described from the Andrarum Limestone. It thus appears that well oxygenated relatively shallow water (inner shelf) was not the preferred habitat of agnostoids whereas trilobites thrived. This biofacies is not represented in the study area.

As remarked above, the thin bioclastic limestones are a facies that formed in relatively shallow water only in the aftermath of major sea-level lowstands. The inner shelf was a sedimentary by-pass zone most of the time, without sedimentary (or fossil) record (see Nielsen & Schovsbo 2015, pp. 299–301).

Biofacies II: Dysoxic shale facies with trilobites

The Miaolingian Alum Shale of Scania–Bornholm and Västergötland is well-known for its rich fossil faunas dominated by common and diverse agnostoids associated with a number of trilobites (Fig. 11). There is stratigraphic variability due to evolutionary changes as well as environmental fluctuations (notably sea-level changes, Fig. 12). Thus, only a few trilobite taxa have been reported from the *G. nathorsti* Zone and trilobites are also very rare in the *A. pisiformis* Zone across southern Scandinavia. The latter level is here classified as biofacies III (see below) and it is possible the *G. nathorsti* Zone of south-central Sweden and Scania also represents this facies. However, for the time being it is interpreted as biofacies II (Fig. 12). Likewise, the upper part of the *L. laevigata* Zone is devoid of trilobites in Scania–Bornholm, whereas a relatively diverse fauna is known from Västergötland (Wallerius 1896, 1930; Westergård 1953, pp. 36–41; Axheimer *et al.* 2006). Biofacies II is suggested to characterize the inboard part of the Alum Shale facies from just below the storm wave base and a little deeper, i.e. the inner part of the outer shelf (Fig. 11).

Biofacies III: Dysoxic shale facies without or very few trilobites

The Alum Shale in the study area contains a fauna almost exclusively dominated by agnostoids, essentially without trilobites apart from sporadic paradoxidids (this statement refers to levels above the *A. oelandicus* Superzone). We classify this strongly agnostoid-dominated fauna as biofacies III and it is suggested to characterize the most offshore, deep part of the Alum Shale sea (Fig. 11). As remarked above, this facies is encountered also at certain stratigraphic levels in southern Scandinavia, where it was introduced during periods with high sea level (Fig. 12).

Discussion

The shelly Miaolingian fauna described here from the Lower Allochthon, classified mainly as biofacies III (Fig. 12), is dominated strongly by agnostoids, including both cosmopolitan species as well as taxa endemic to Scandinavia. Except for one new species, all taxa are known from coeval strata in southern Scandinavia but there are a number of differences with regard to overall frequency of the individual species (see below). Trilobites, on the other hand, are very rare in the study area except for paradoxidids. This general absence stands in strong contrast to the mixed trilobite/agnostoid faunas known from southern Scandinavia and the Oslo Region (for references, see Appendix 1), from levels representing biofacies I and

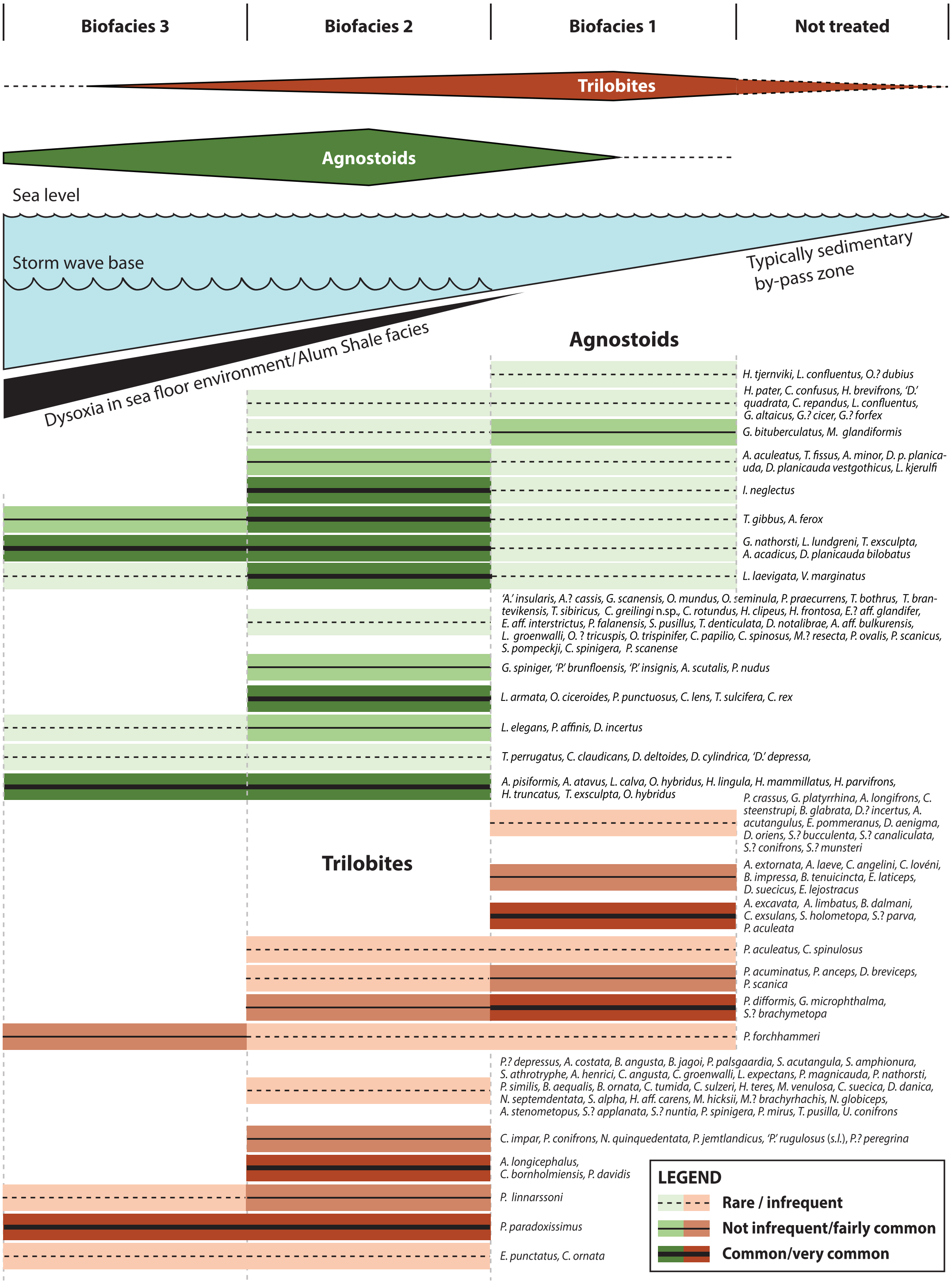


Fig. 11. Biofacies in the *P. paradoxissimus* and *P. forchhammeri* superzones of Scandinavia. The assessment of palaeoenvironmental distribution of agnostoid and trilobite species is based mainly on the occurrences reported by Westergård (1946, 1948, 1950, 1953), Høyberget & Bruton (2008), Weidner & Nielsen (2014) and present study, see also Figure 12. The indicated frequency for each species is the most common presence recorded in Scandinavia. The upper part of the diagram showing the general distribution of agnostoids and trilobites in general along a depth transect is constructed by counting the number of taxa in each biofacies that are categorized as 'not infrequent' and 'common' and the latter category has been given double weight, whereas rarities have been ignored. The combined number of 'not infrequent' and 2 x 'common' taxa has been multiplied with the arbitrary factor 0.2 (in order to produce an appropriate size of the illustration) and the resulting figure = the height of the frequency in mm for agnostoids and trilobites in the middle of the respective biofacies. It is clearly seen that agnostoids are most common in biofacies 2 (upper dysoxic environment) whereas trilobites are more common in the well-ventilated biofacies 1. The boundary between biofacies 1 and 2 is probably sharper than indicated, as it marks the transition from a well-ventilated sea-floor environment to an oxygen reduced environment, whereas the transition from biofacies 2 to 3 likely is gradual and the boundary is, hence, arbitrary.

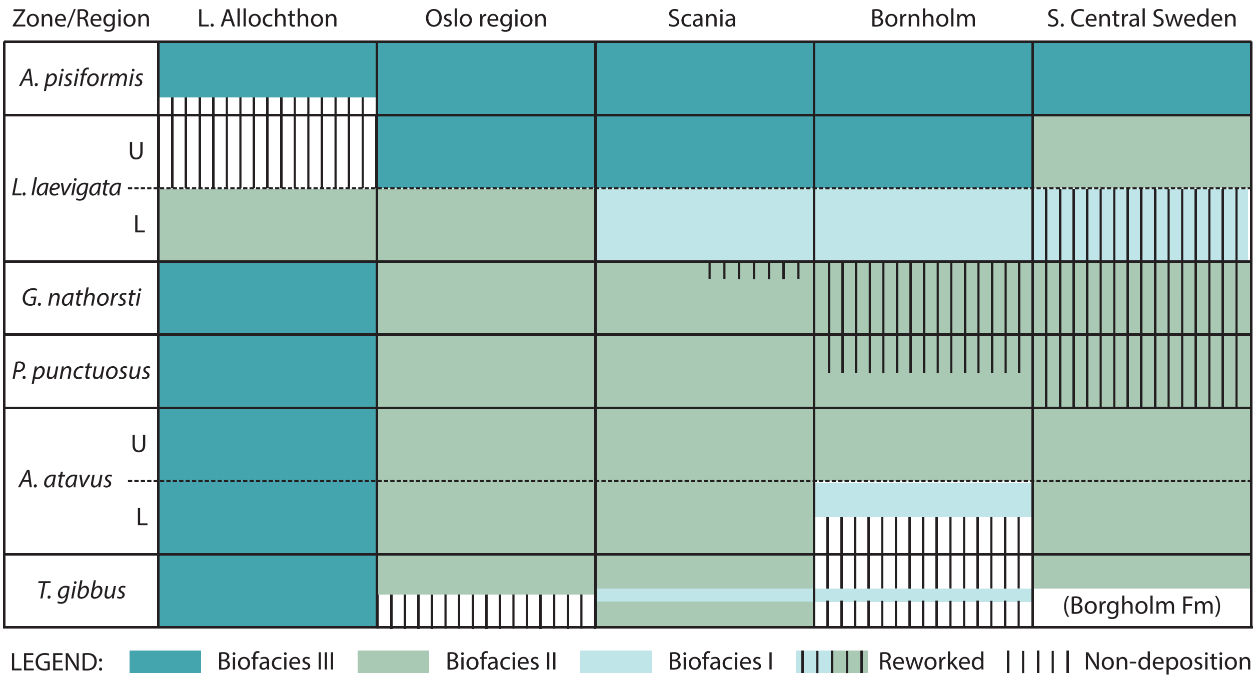


Fig. 12. Assessment of temporal biofacies distribution in Scandinavia; the main controlling factor for the observed changes was sea level variations. It is possible that the *G. nathorsti* Zone of Scania-Bornholm should be classified as biofacies III and much of the succession in the Oslo Region below the *L. laevigata* Zone may be regarded as transitional between biofacies II and III. The scheme is a key to the biofacies classification of the species listed in Fig. 11.

II (Fig. 12). The only exception to this general absence of trilobites is seen in the lower part of the *L. laevigata* Zone at Abborrfallet in the southern part of the study area, where several species of trilobites are recorded (see also Asklund & Thorslund 1935). This horizon may be taken as an impoverished biofacies II. A generally very low sea level prevailed during the early part of the *L. laevigata* Zone, creating gaps across the shelf in large parts of Sweden that now came within reach of storm waves (Exporrecta Conglomerate). At this time, the Andrarum Limestone (biofacies I) formed in Scania-Bornholm and elsewhere in southern Scandinavia, connected with pulses of incipient sea level rise. Coeval shales are known only from western Scandinavia (study area and Krekling in the Oslo Region).

The described agnostoid fauna differs from that of southern Scandinavia (Appendix 2) in being of lower diversity and by lacking genera originally described from the Barrandian area including *Phalagnostus*, *Pleuroctenium* and *Skryjagnostus*. Representatives of these taxa occur sporadically in the *A. atavus* Zone in Scania and south-central Sweden as well as on Bornholm, Denmark (Westergård 1946; Weidner & Nielsen 2014). At lower stratigraphic level, the 'Barrandian' *Condylopyge* and *Dawsonia*, known from the *A. pinus* – *P. praecurrens* Zone of Öland, are also absent.

Among 'Scandinavian' agnostoids, the stratigraphically important *Tomagnostus fissus* and *Ptychagnostus punctuosus* that are both very common in Scania and on Bornholm, were not encountered in the Lower Allochthon and genera like *Onymagnostus*, *Tomagnostus* and *Cotalagnostus* are overall poorly represented. *Onymagnostus ciceroides* (Matthew, 1896), *O. seminula* (Whitehouse, 1939), *T. sibiricus* Pokrovskaya & Egorova, 1972, *C. lens* (Grönwall, 1902), and *Acadagnostus scutalis* (Hicks, 1872) that are known from southern Scandinavia, notably Scania-Bornholm, have not been found and neither have a few Scandinavian endemics, such as *Hypagnostus frontosa* (Grönwall, 1902), *Cotalagnostus rotundus* (Grönwall, 1902), and *Svenax pusillus* (Tullberg, 1880). These taxa all seem to be limited to biofacies II.

The composition of the agnostoid fauna in Lapland also differs in other ways from that of southern Scandinavia. *Doryagnostus incertus*, occurring in the *P. punctuosus* Zone, is more widespread than in southern Scandinavia (cf. Westergård 1946). *Lejopyge* *calva*, occurring in the *G. nathorsti* Zone, is also very common in biofacies III. It is known also from the Oslo Region, where it likewise is common at a couple of localities (Høyberget & Bruton 2008). This species has not been reported previously from Sweden, but it may have been confused with *L. laevigata*. Two other species that are very rare in southern Scandinavia occur abundantly, viz. *Hypagnostus truncatus* and *Hypagnostus lingula*, and the latter is one of the most common species in the *A. atavus* Zone of the Lower Allochthon. Conversely, *Triplagnostus gibbus*, *Tomagnostus perrugatus* and *Acadagnostus acadicus* that all are abundant in the south, are infrequent in the study area.

Some of the differences regarding diversity and distribution of agnostoid taxa may be adventitious, because there are fewer localities and limited exposures and, hence, less collecting effort in the study area compared to southern Scandinavia, but there is still a clear difference in diversity and abundance of several species. The general absence of trilobites and the reduced diversity of the agnostoid fauna in the Lower Allochthon are therefore real phenomena. It is also seen that the diversity of genera and species decreases northwards in the study area. As remarked elsewhere, this may to some extent be related to the decreased presence of limestone in the Alum Shale in that direction (see section 'New studies of the Lower Allochthon'), but we also infer that the palaeoenvironment broadly speaking deepened northwards (in fact, probably westwards, but the mountain range provides an oblique cross section of the palaeo-shelf). This deepening is assumed at least partly responsible for the decreased faunal abundance observed. Highstand intervals (? = low oxygen periods) in the Miaolingian Alum Shale of southern Scandinavia also exhibit a very low diversity, notably in the *A. pisiformis* Zone, marking the highest Cambrian sea-level stand in Scandinavia, at a time where the Alum Shale facies extended all the way to Gotland (cf. Ahlberg 1989).

Miaolingian trilobite faunas have been described from allochthonous strata in southern Norway by Strand (1929), Ebbestad & Budd (2003) and Høyberget & Bruton (2008). Trilobites are fairly represented, especially in beds equivalent in age to the Exsulans and Andrarum Limestone beds (i.e. sea-level lowstand intervals). These Norwegian faunas are, however, less diverse than those described from Scania and much of the succession may be classified as transitional between biofacies II and III. The expanded lower part of the *L. laevigata* Zone at Krekling (see Brøgger 1878; Høyberget & Bruton 2008) seems to represent biofacies II, a deeper water facies coeval with the Andrarum Limestone Bed of Scania-Bornholm (biofacies I), characterizing a shallower, more inboard setting on the palaeo-shelf. The agnostoid taxa recorded from the Miaolingian of southern Norway are by and large comparable to those collected in our study area. Noticeable is the abundant presence of *L. calva* in the *G. nathorsti* Zone and the near lack of *P. punctuosus*. *Lejopyge laevigata* is common throughout the eponymous zone in Norway whereas only very few specimens of this species were found in Lapland.

The allochthonous Miaolingian strata of the Digermulen Peninsula in northern Norway have a restricted fossil record including a few trilobites and two agnostoid taxa, *Doryagnostus incertus* and *Acadagnostus ferox*, both shared with the study area (cf. Nikolaisen & Henningsmoen 1990). The fauna is too meager to allow distinction of biofacies.

Our rough biofacies analysis focuses on the *P. paradoxissimus* and *P. forchhammeri* superzones. The older *A. oelandicus* Superzone of Öland has yielded a quite rich fauna (Westergård 1936), dominated by trilobites but including a few species of agnostoids as well (the low diversity of agnostoids may reflect their early stage of evolution). This is a relatively inboard fauna, but even so, it probably represents a setting below storm wave base. In the Lower Allochton of the study area, the diversity of agnostoids and trilobites is significantly lower at this stratigraphic level, and the latter group is dominated strongly by paradoxidids. This is a more offshore facies than developed on Öland, as remarked by Weidner *et al.* (2014, pp. 517–518).

The three Scandinavian biofacies in the *P. paradoxissimus* – *P. forchhammeri* interval are closely comparable with the distribution of Miaolingian faunas in Tasmania, Australia, described by Jago (1973). He distinguished (1) an 'open sea' agnostid assemblage, in which trilobites are absent or rare, (2) a mixed ptychagnostid-non-nepeid assemblage containing both agnostoids and trilobites, and (3) a nepeid-clavagnostid-peronopsid assemblage, which does not contain ptychagnostids whereas trilobites are abundant. Jago (1973) suggested that the Tasmanian faunal distribution reflects an offshore-nearshore transect, with absence of trilobites, considered benthic, in the offshore assemblage (he considered agnostoids as pelagic). The offshore assemblage 1 is of low diversity, dominated by ptychagnostids (often effaced) and only *Onymagnostus hybridus* [reported as *P. stenorrhachis*] and *Hypagnostus* aff. *H. parvifrons* were named; both species are common in biofacies III in our study area. Assemblage

2 contains a mix of agnostoids and trilobites, and brings biofacies II in Scandinavia to mind. However, the reported species composition is difficult to compare directly with Scandinavia as the only Tasmanian fauna described derives from the lower part of the *L. laevigata* Zone, which was a time with very low sea level. This caused non-deposition and erosion across much of south-central Sweden, and the Scandinavian fossil record is dominated by biofacies I in Scania-Bornholm (Andrarum Limestone Bed). The Tasmanian assemblage 3, taken to represent the most inboard setting, contains common trilobites, *Clavagnostus* and '*Peronopsis*' whereas ptychagnostids are absent (Jago 1973). Representatives of *Clavagnostus* are rare in Scandinavia and reported only from the Andrarum Limestone (biofacies I) in Scania and the uppermost part of the *L. laevigata* Zone in Västergötland (biofacies II, very rare). The distribution of *Peronopsis* cannot be discussed as it is a waste-basket designation.

Conclusions

The present study gives the first comprehensive description and analysis of the Miaolingian (middle Cambrian) agnostoid–trilobite fauna from the Alum Shale Formation in the Lower Allochthon Blaik Nappe Complex of the Swedish Caledonides. The investigated displaced successions were deposited on the distal outer shelf of Baltica, facing the Iapetus Ocean, several 100's of kilometres west of their current location.

More than 1000 specimens, mostly disarticulated sclerites, have been collected from 46 localities along a 200 km long stretch of the mountain chain from Jämtland to Lapland in NW Sweden, and several new localities are recorded in this study. Due to the strong tectonic overprint, many of the fossils are distorted and stratigraphic sections could not be measured and collected bed-by-bed. In addition, the fossils derive solely from limestone concretions and beds (so-called orsten), and not from the shale lithology, in which they have been dissolved, just as they have across much of mainland Sweden. For unknown reasons, orsten (and, hence the chance of finding fossils) become rare northwards in the area.

The collected material contains an agnostoid-paradoxidid fauna comprising 39 agnostoid and 17 trilobite taxa. The fauna is dominated strongly by agnostoids and among trilobites, only paradoxidids with 6 taxa are relatively common. One species, *Cotalagnostus greilingi* n. sp., is new while *Lejopyge calva*, *Hypagnostus clipeus*, *Doryagnostus deltoides* and *Lisogoragnostus confluentus* are reported for the first time from Sweden. The remaining taxa are known also from southern Scandinavia, but the fossil assemblage in the Lower Allochthon is of lower diversity and the relative composition differs. Thus, *Lejopyge calva*, *Hypagnostus lingula*, *Hypagnostus truncatus* and *Doryagnostus incertus* are much more common in the studied fauna than in southern Scandinavia whereas *Triplagnostus gibbus*, *Acadagnostus acadicus*, *Tomagnostus fissus*, *Cotalagnostus lens* and *Ptychagnostus punctuosus* are relatively rare or absent. Further, agnostoids and trilobites from other continents like Avalonia, Bohemia, Siberia or Australia, occasionally found in southern Scandinavia, are missing except for findings of *D. deltoides* and one pygidium of *Kootenia*. New material of *Homagnostus pater*, *Onymagnostus hybridus*, *Triplagnostus gibbus*, *Tomagnostella exsculpta* and *Lisogoragnostus confluentus* adds to the understanding of these taxa.

The studied fauna represents the *Pentagnostus praecurrens*, *Triplagnostus gibbus*, *Acidusus atavus*, *Ptychagnostus punctuosus*, *Goniagnostus nathorsti*, *Lejopyge laevigata* and *Agnostus pisiformis* agnostoid zones. The basal Miaolingian Hawke Bay hiatus is extensive in the area and comprises the Kibartian and lowermost part of the Bödan stages up to and including the *Eccaparadoxides insularis* Zone. In addition to this major hiatus, no fossils characteristic of the upper part of the *L. laevigata* Zone have been found, suggestive of uplift of the northwestern margin of Baltica in the late Miaolingian. The overlying *Agnostus pisiformis* Zone has also been found only at a few sites in the Exporrecta Conglomerate. This uplift phase was likely connected with contemporaneous plate tectonic changes; no corresponding isostatic disturbances have been described from elsewhere in Scandinavia so far.

Hitherto, the age of the Alum Shale north of Lake Storuman was unknown, but assumed to represent the Miaolingian. Our study confirms for Storvindeln the *A. oelandicus* Superzone (*A. pinus* – *P. praecurrens* Zone) and the lower Tremadocian, and for Gautojaure the *P. forchhammeri* Superzone. It is further likely that the *P. forchhammeri* Superzone is present at Hornavan. All limestones collected will eventually be investigated for microfossils to obtain additional indications for the stratigraphical position of the exposed strata.

Three benthic biofacies are recognized for the Scandinavian *Paradoxides paradoxissimus* and *P. forchhammeri* superzones. Biofacies I is the most inboard facies, characterized by a comparatively diverse and abundant trilobite fauna while agnostoids are infrequent. This facies is taken to represent a well-ventilated sea-floor environment that is not observed in the study area. Biofacies II contains a much more diverse agnostoid fauna, still with some trilobites, but of lower diversity. This facies is suggested to have characterized an upper dysoxic sea-floor environment that was dominant in much of the Miaolingian of south-central Sweden and Scania-Bornholm. This facies is not recorded in the study area, but the lowstand interval in the lower part of the *L. laevigata* Zone may be classified as transitional between biofacies II and III. Biofacies III, the most offshore facies, is the prevalent biofacies in the study area. It is dominated by agnostoids with infrequent or no trilobites and is taken to characterise a low oxygen level sea floor environment which may be classified as low dysoxic.

Systematics

Trilobites are generally described in alphabetical order: families, genera, species. For the agnostoids we follow the generic concept and order of Shergold & Laurie (1997), unless otherwise stated. Abbreviations OD and SD are used for 'Original designation' and 'Subsequent designation', respectively. Occurrences are described as dominant, abundant, common, infrequent and rare. Magnification factor for illustrated agnostoids is, except for some small-sized species and close-up of details, the same in most illustrations for easy comparison. Where a larger magnification is used, this is emphasized in the captions. Different magnification factors are applied for trilobites, but for the same sclerites we always use the same factor in individual illustrations. For some species, material from Västergötland, Scania and ice-rafted boulders of Denmark is illustrated to assist the taxonomic descriptions. These specimens are in our photographic illustrations shown with a white letter on black background.

Repositories. – BMNH (Natural History Museum, London, UK); GSC (Geological Survey of Canada, Ottawa, Ontario, Canada); LO (Lund Original, Department of Geology, Lund University, Sweden); MGUH (Natural History Museum of Denmark, University of Copenhagen); MK (Müritzeum, Waren, Germany; collection Buchholz); NRM (Naturhistoriska Riksmuseet, Swedish Museum of Natural History, Stockholm); PMO (Palaeontological collections of the Natural History Museum, University of Oslo, Norway); PMU (Palaeontological collections, Museum of Evolution, Uppsala University, Sweden); SGU/SGUR (Geological Survey of Sweden); USNM (United States National Museum, Washington DC, USA).

Family Agnostidae McCoy, 1849

Genus *Agnostus* Brogniart, 1822

Type species (SD, Jaekel, 1909). – *Entomostracites pisiformis* Wahlenberg, 1818, from the *Agnostus pisiformis* Zone, Alum Shale Formation on Mount Kinnekulle, Västergötland, Sweden.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Only one species, *A. pisiformis* (Wahlenberg, 1818), is reported from the Miaolingian of Scandinavia.

Agnostus pisiformis (Wahlenberg, 1818)

Figure 13

1818 *Entomostracites pisiformis* Wahlenberg, p. 42, pl. 1, fig. 5.
1822 *Agnostus pisiformis* (Wahlenberg); Brongniart, p. 38, pl. 4, fig. 4.
1827 *Battus pisiformis*; Dalman, p. 258, pl. 6, fig. 5a–d.
1837 *Battus pisiformis*; Hisinger, p. 19, pl. 4, fig. 5.
1851 *Agnostus pisiformis* (Linnaeus); Angelin, p. 7, pl. 6, fig. 7.
1869 *Agnostus pisiformis* (Linnaeus); Linnarsson, p. 81, pl. 2, figs 50–51.
1869 *Agnostus pisiformis* (Brongniart); Karsten, p. 75, pl. 25, fig. 7.
1874 *Agnostus pisiformis* (Brongniart); Steinhardt, p. 61, pl. 4, fig. 16.
1878 *Agnostus pisiformis* Angelin; Brøgger, pl. 6, fig. 13a, b.
1880 *Agnostus pisiformis* (Linnaeus); Tullberg, p. 25, pl. 2, fig. 14a, b.
1885 *Agnostus pisiformis* (Brongniart); Roemer, p. 32, pl. 1, fig. 6a–c.
1890 *Agnostus pisiformis* (Linné); Pompeckj, p. 14, pl. 4, fig. 23.
1906 *Agnostus pisiformis* (Linnaeus); Lake, p. 9, pl. 1, fig. 12.
1908 *Agnostus pisiformis* (Linnaeus); Mordziol, p. 535, text fig. 1.
1909 *Agnostus pisiformis*; Jaekel, p. 399, fig. 18.
1922 *Agnostus pisiformis* (Linnaeus); Westergård, p. 115, pl. 1, figs 1–3.
1923 *Agnostus pisiformis* Linné; C. Poulsen, p. 21, pl. 1, fig. 1.
1946 *Agnostus pisiformis* (Linnaeus); Westergård, p. 85, pl. 13, figs 10–14.
1946 *Agnostus pisiformis spiniger* (Dalman); Westergård, p. 86, pl. 13, figs 15, 16.
1946 *Agnostus pisiformis subsulcatus* subsp. n. Westergård, p. 86, pl. 16, figs 4, 5.
1958 *Agnostus* (*Agnostus*) *pisiformis* (Linnaeus); Henningsmoen, p. 181, pl. 5, figs 1–12.
1962 *Agnostus pisiformis* (Linnaeus); Hutchinson, p. 86, pl. 12, figs 2–6.
1967 *Agnostus pisiformis* (Linné); Hucke & Voigt, p. 50, pl. 7, fig. 1.
1976 *Agnostus pisiformis* (Wahlenberg); Reyment, p. 3, fig. 3a, b.
1978 *Agnostus pisiformis pisiformis* (Wahlenberg); Rushton, p. 258, pl. 24, figs 15–19.
1987 *Agnostus pisiformis* (Linnaeus); Müller & Walossek, p. 1, figs 1–28, pls 1–33.

1988 *Agnostus pisiformis pisiformis* (Wahlenberg); Martin & Dean, p. 15, pl. 5, figs 1–4, 7, 9.
1989 *Agnostus pisiformis* (Wahlenberg); Ahlberg, p. 142, fig. 5A–C.
1990 *Agnostus* (*Agnostus*) *pisiformis* (Wahlenberg); Shergold, Laurie & Sun, p. 72, fig. 9:1.
1991 *Agnostus pisiformis* (Linnaeus); Buchholz, p. 110, pl. 1, figs 8, 9, textfigs 2A, 3A.
1991 *Agnostus pisiformis* (Linnaeus); Lendzion & Orlowski, p. 44, pl. 10, figs 1, 2.
1992 *Agnostus pisiformis* (Linnaeus); Rudolph, p. 159, pl. 1, figs 1–6; pl. 2, figs 1–5.
1994 *Agnostus pisiformis* (Linnaeus); Rudolph, p. 105, pl. 1, figs 1–3; pl. 2, figs 3, 4.
1996 *Agnostus pisiformis* (Wahlenberg); Ahlberg & Ahlgren, p. 130.
1997 *Agnostus* (*Agnostus*) *pisiformis* (Wahlenberg); Shergold & Laurie, fig. 217:1a, b.
1999 *Agnostus pisiformis pisiformis* (Wahlenberg); Buchholz, p. 240, pl. 1, figs A, B.
1999 *Agnostus pisiformis dissimilis* n. ssp. Buchholz, p. 240, pl. 1, figs F, G.
1999 *Agnostus pisiformis spiniger* (Dalman); Buchholz, p. 241, pl. 1, figs C, D.
1999 *Agnostus pisiformis subsulcatus* Westergård; Buchholz, p. 242, pl. 1, fig. E.
1999 *Agnostus procerus* n. sp. Buchholz, p. 243, pl. 1, figs I, J.
2000 *Agnostus pisiformis pisiformis* (Wahlenberg); Buchholz, p. 705, pl. 1, figs 1, 2; textfig. 1A.
2000 *Agnostus pisiformis dissimilis* Buchholz; Buchholz, p. 714, pl. 1, figs 5–8; textfig. 1C.
2000 *Agnostus pisiformis spiniger* (Dalman); Buchholz, p. 714, pl. 1, fig. 3, 4; textfig. 1B.
2000 *Agnostus pisiformis vastificus* n. ssp.; Buchholz, p. 715, pl. 1, figs 9–11; textfig. 3.
2000 *Agnostus procerus* Buchholz; Buchholz, p. 717, pl. 2, figs. 2–5, 8; textfig. 5B.
2002 *Agnostus pisiformis pisiformis* (Wahlenberg); Schöning, fig. 16.
2006a *Agnostus* (*Agnostus*?) *confusus* n. sp. Mischnik, p. 2, fig. 1.
2006b *Agnostus* (*Agnostus*) *distinctus* n. sp. Mischnik, p. 3, pl. 1; textfigs 1, 2.
2008 *Agnostus pisiformis* (Wahlenberg); Høyberget & Bruton, p. 19, pl. 1, figs G–N.
2014 *Agnostus pisiformis* (Wahlenberg); Danukalova, Kuzmichev & Korovnikov, p. 361, pl. 3, figs 12, 13.
2016 *Agnostus pisiformis* (Wahlenberg); Buchholz, p. 336, fig. 5A, B.

Lectotype (designated by Shergold et al. *1990)*. – Cephalon, PMU vg 819a, originally figured by Wahlenberg (1818, pl. 1, fig. 5) and refigured by Shergold & Laurie (1997, fig. 217:1a). The specimen derives from the eponymous zone at Hönsäter, Kinnekulle, Västergötland, Sweden.

Paralectotype. – Pygidium, PMU vg 819b, from the same block as the lectotype. Hence, it is not from Billingen, Västergötland, as stated by Shergold & Laurie (1997, fig. 217:1b).

Material and occurrence. – About 10 cephala and pygidia were found in a loose block of the Exporrecta

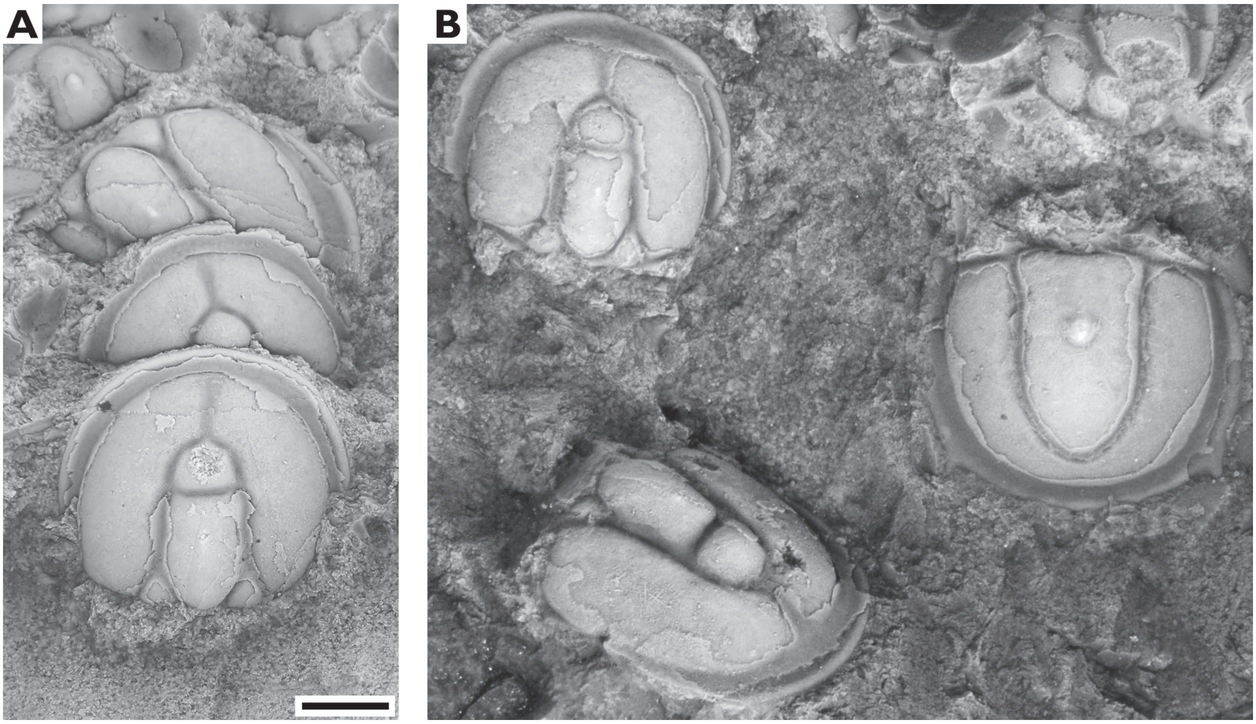


Fig. 13. ***Agnostus pisiformis*** **(Wahlenberg, 1818)**, from the Exporrecta Conglomerate Bed at Skansholm. **A**, group of three cephala. PMU 36409/1. **B**, group of two cephala and one pygidium. PMU 36409/2–4. Scale bar = 1 mm. Note that the magnification is larger than used for most agnostoid illustrations in this publication.

Conglomerate Bed on the shore at Skansholm, and the conglomerate thus seems to represent the *A. pisiformis* Zone. Kulling (1955) recorded *A. pisiformis* and *Oligomys exporrecta* from the same locality as well as from Djupdal. From northern Jämtland and the Tåsjö Mountain, the conglomerate is reported from Siljeåsen and Sågbäcken (Asklund & Thorslund 1935). *Agnostus pisiformis* occurs abundantly in Sweden, Norway, Denmark (Bornholm), Germany (ice-rafted boulders), Poland (Žarnowiec borehole), Avalonian Great Britain (England), Avalonian Canada (eastern Newfoundland) and Siberia (Bennett Island) (Lake 1906; Westergård 1922, 1946; C. Poulsen 1923; Hutchinson 1962; Lendzion & Orlowski 1991; Rudolph 1994; Høyberget & Bruton 2008; Danukalova *et al*. 2014). The species occurs sparsely in the upper *L. laevigata* Zone, but in the *A. pisiformis* Zone it is the most common agnostoid species.

Remarks. – Both the cephalon and the pygidium display considerable variations especially in the surface sculpture, but also in the distinctness of preglabellar and axial furrows, the general width-length relations and spinosity. Westergård (1946) recognized two subspecies, *A. pisiformis spiniger* (*A. pisiformis* Zone) and *A. pisiformis subsulcatus* (*P. forchhammeri* Superzone), whereas Mischnik (2006a, 2006b) and Buchholz (1991, 1999, 2000, 2016) took an even more restricted view and separated several additional species and subspecies collected from ice-rafted boulders (*A.*? *confusus*, *A. distinctus*, *A. procerus*, *A. pisiformis dissimilis*, *A. pisiformis vastificus* and other forms treated under open nomenclature, all from the *A. pisiformis* Zone). We consider these as intraspecific variations (cf. Høyberget & Bruton 2008). The new cephala have wide border furrows and a distinct preglabellar furrow, and the pygidia have the axial furrows faintly indicated only laterally. Our specimens thus correspond exactly to the illustrations of material from Västergötland and Norway published by Westergård (1946) and Høyberget & Bruton (2008), respectively.

Genus *Homagnostus* Howell, 1935c

Type species (OD). – *Agnostus pisiformis* Linnaeus var. *obesus* Belt, 1867, from the Lower Lingula Flags of North Wales, *Olenus* Superzone, United Kingdom.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Only one species, *H. pater* (Westergård in Holm & Westergård, 1930), occurs in the Miaolingian of Scandinavia.

Homagnostus pater (Westergård *in* Holm & Westergård, 1930)

Figure 14A–T

1930 *Agnostus pisiformis pater* n. subsp. Westergård *in* Holm & Westergård, p. 9, ?pl. 1, fig. 1; pl. 4, figs 9–10.
1940 *Homagnostus pater* (Holm & Westergård); Lermontova, p. 124, pl. 36, fig. 3, 3a.
1946 *Agnostus pater* Westergård; Westergård, p. 84, pl. 13, figs 4–6.
2004 *Agnostus pater* Westergård; Weidner, Ahlberg, Axheimer & Clarkson, p. 44.
non 2006 *Agnostus pater*; Axheimer, Eriksson, Ahlberg & Bengtsson, fig. 6l [= indet.].
non 2008 *Homagnostus* cf. *pater* (Westergård); Ergaliev & Ergaliev, p. 37, pl. 28, fig. 26 [= indet.].

Holotype (OD). – Pygidium, NRM Ar9544, originally figured by Westergård *in* Holm & Westergård (1930, pl. 4, fig. 10) and re-illustrated by Westergård (1946, pl. 13, fig. 5). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Kiviks-Esperöd, Scania, Sweden.

Material and occurrence. – Two cephala, 2.6 mm and 2.5 mm long, were collected from one block at Skansholm. They are associated with *Cotalagnostus greilingi* n. sp. and pleural fragments of a paradoxidid (*P. forchhammeri*?). Only blocks of the *P. forchhammeri* Superzone were found at this locality, and we confidently assign the two cephala to this superzone, most likely deriving from the lower part of the *L. laevigata* Zone as in southern Scandinavia. The rare and small *H. pater* is known only from the Swedish districts Scania, Västergötland, Närke and Öland (Westergård 1946), where it occurs in the Andrarum Limestone and Exporreta Conglomerate beds. More than 50 well-preserved cephala and pygidia were collected from two ice-rafted boulders at As Hoved, Denmark, in Andrarum Limestone with provenance from Västergötland (Weidner *et al*. 2004) (here illustrated in Fig. 14C–R). As Westergård (1946) illustrated only one cephalon and two pygidia, a supplementary description of *H. pater* is presented based on this material to elucidate intraspecific variation.

Description. – Most shields are 3 to 4 mm long. The cephalon has a moderately tapering glabella with expanded M2 and abaxially short and distinct constrictions at F2; F3 is deep and narrow. A small node is situated anteriormost on M2. The anteroglabella is rounded or vaguely pointed. The basal lobes are large and connected by a narrow band, the cheeks taper forwards to almost half the posterior width and they are separated by a continuous median preglabellar furrow of variable width (Fig. 14A–I). The anterior

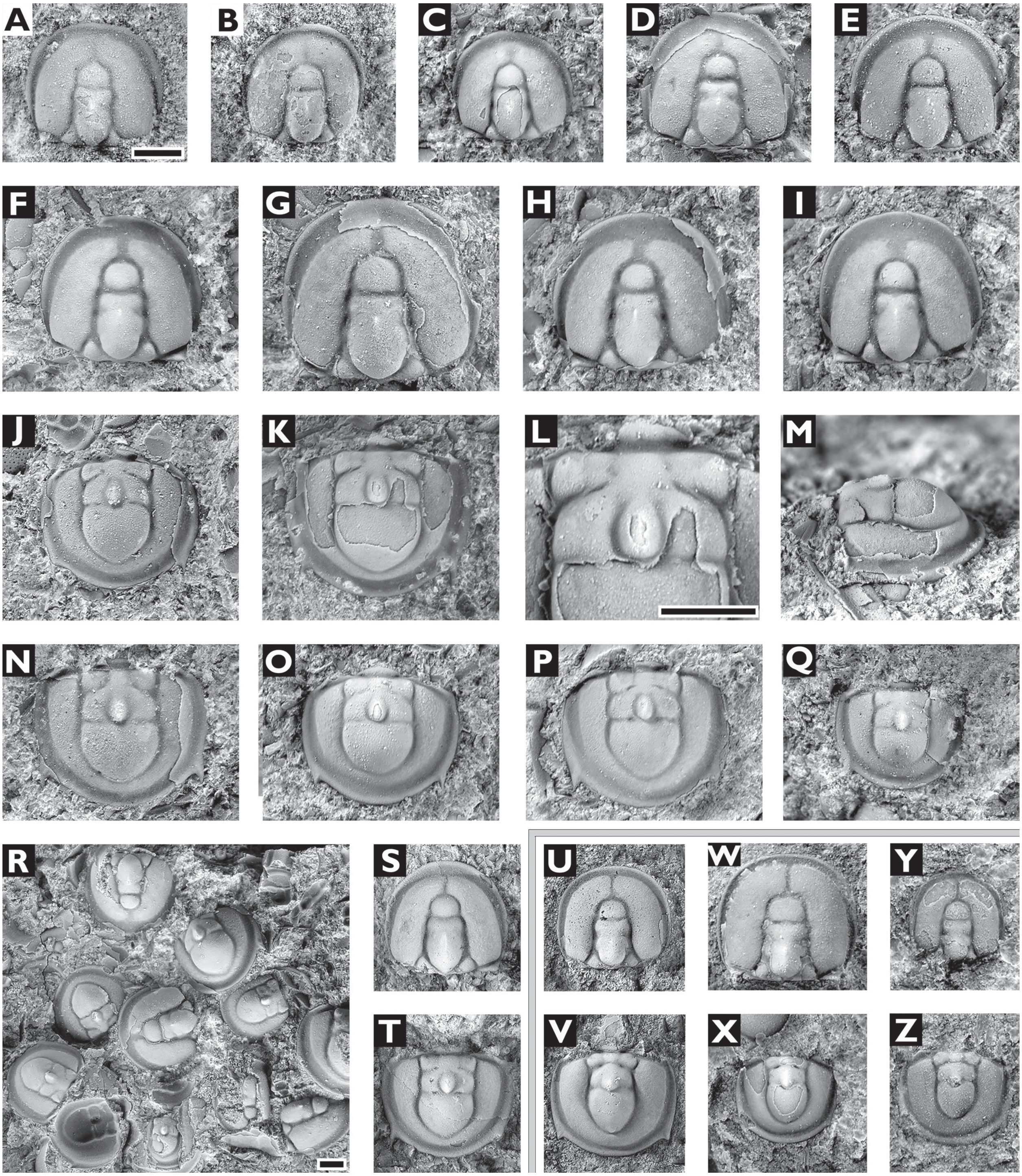


Fig. 14. ***Homagnostus pater*** **(Westergård in Holm & Westergård, 1930)**, lower part of the *L. laevigata* Zone. **A**–**B**, cephala, Skansholm. PMU 36412/1, 36414. **C**–**I**, cephala, with progressively wider median preglabellar furrow, ice-rafted boulder, As Hoved, Denmark. MGUH 34015–34021. **J**–**Q**, pygidia, ice-rafted boulder, As Hoved, Denmark. **L**, close up view of K to display structure of M1 and M2; **M** side view of the same specimen. MGUH 34022–34027. **R**, group of cephala and pygidia, ice-rafted boulder, As Hoved, Denmark. MGUH 34028. **S**–**T**, cephalon and **holotype** pygidium of *Homagnostus pater* (originally figured by Westergård in Holm & Westergård (1930, pl. 4, fig. 10) and re-illustrated by Westergård (1946, pl. 13, fig. 5)). NRM Ar9543, NRM Ar9544. ***Innitagnostus neglectus*** **(Westergård, 1946)**, to illustrate differences in comparison with *Homagnostus pater*. **U**–**V**, **holotype** cephalon and pygidium from Gudhem, Västergötland. Upper part of *L. laevigata* Zone. Previously illustrated by Westergård (1946, pl. 13, figs 7 and 8). SGU 4973, SGU 4974. **W**, cephalon from Gudhem, Västergötland. PMU 37230. **X**, pygidium from Vilske, Västergötland. PMU 37231. **Y**–**Z**, cephalon and pygidium from ice-rafted boulders, As Hoved, Denmark. Lower part of *L. laevigata* Zone (Exporrecta Conglomerate). MGUH 34029–34030. Scale bars = 1 mm.

border can be extremely wide and concave and narrows towards the rear (Fig. 14G–I). The highest point of the glabella is at about mid-length. The pygidial axis is parallel-sided with almost no constrictions at F1 and F2. The anteroaxis and the posteroaxis have the same length; the tip of the posteroaxis is rounded or slightly pointed. F1 is only laterally impressed and directed forwards; thus, the medial part of M1 appears as an anterior extension of M2 (Fig. 14L). F2 is straight. A prominent and long axial node on M2 reaches F2 or just slightly beyond. The pleural fields are confluent behind the axis, the postaxial field is relatively wide and the border furrow is wide and concave all around, but not as wide as the cephalic border furrow. A pair of sharp lateral spines is situated level with the tip of axis and directed straight backwards. A salient diagnostic feature of *H. pater*, according to Westergård (1946), is the almost straight articulating margin of both shields; this is particularly visible in the pygidium (see Westergård 1946, pl. 13, figs 4–6). In the new material, this feature is not as distinct.

Discussion. – Westergård (1946) assigned *pater* to *Agnostus*, due to the similarity of its cephalon with that of *A. pisiformis*. The two species differ by the more strongly pronounced segmentation of the pygidial axis in *pater*. Other authors allocated *pater* to *Homagnostus* based on agreement of the cephalon, but also on several traits of the pygidium, which displays closer relationship with *Homagnostus* than with *Agnostus*, notably the type species *H. obesus*. Our study of well-preserved material of *H. pater* from As Hoved showed complete correspondence in the structure of the pygidial M1 and F1 with *H. obesus*: F1 is only laterally impressed while the medial part of M1 appears as a mere extension of M2 (Fig. 14L; Buchholz 2004b, fig. 1B, pl. 1b, c, e, pl. 2k; Ahlberg & Terfelt 2012, fig. 3c, e; Buchholz 2016, fig. 11B). In *pisiformis*, F1 is effaced or faint, but continuous. Further, *pater* possesses the elongate axial node typical for *Homagnostus*; in *Agnostus* the node is prominent, but rounded. We therefore assign *pater* to *Homagnostus*.

Homagnostus pater thus closely resembles *H. obesus* from the Furongian *Olenus* Superzone but differs in the cephalon usually having a wider border and median preglabellar furrows, although illustrations of *obesus* show some variability in these features (Pratt 1992, pl. 1, figs 26, 30, 31 [wide border furrow, indistinct median preglabellar furrow]; Buchholz 2004b, pl. 1a versus 1d [wide and narrow border furrows]; Ahlberg & Terfelt 2012, fig. 3c [wide border and median preglabellar furrows]; Buchholz 2016, fig. 11A [wide border furrow, indistinct median preglabellar furrow]). In the pygidium, *obesus* generally has a narrower border furrow, a wider axis and consequently narrow pleural fields, a posteroaxis longer than the anteroaxis, a more swollen posteroaxis, a narrow postaxial field and an axial node extending beyond F2. As in the cephalon, also the pygidium of *obesus* displays variability in these features, with exception of the axis, which is constantly wider in *obesus* than in *pater* (Rushton 1983; Pratt 1992; Buchholz 1999, 2000, 2004b, 2016; Ahlberg & Terfelt 2012). These intraspecific variations in *obesus* strengthen evidence for the assignment of *pater* to *Homagnostus*.

The pygidium of *Agnostus pater* from Bennett Island, Siberia, illustrated by Westergård *in* Holm & Westergård (1930, pl. 1, fig. 1), is slightly damaged but may represent this species, although it has an axis considerably narrower than is typical of *H. pater* and the posteroaxis is longer than the anteroaxis. These traits have not been observed in our extensive material from As Hoved. The Siberian pygidium agrees, however, in having a medially effaced F1.

The pygidium from Kazakhstan, assigned to *Homagnostus* cf. *pater* by Ergaliev & Ergaliev (2008), has a narrow axis and a pointed tip of the posteroaxis and we do not consider it to belong to *H. pater*.

Axheimer *et al.* (2006) figured a pygidium assigned to *Agnostus pater* from the upper part of the *L. laevigata* Zone at Gudhem, Västergötland. The posteroaxis is longer than the anteroaxis, the border furrow is comparatively narrow and F1 is transverse, all features not found in *H. pater*.

Agnostus neglectus Westergård, 1946 also occurs in the *L. laevigata* Zone (lower and upper parts) in Scania, Västergötland and Närke (Westergård 1946) and in ice-rafted boulders at As Hoved, Denmark (Fig. 14U–Z). The cephalon differs from *H. pater* by having a parallel-sided and distinctly segmented posteroglabella, the cheeks have the same width throughout and the border furrow is deep and of even width. The glabellar node is situated at the posterior end of M2. Pygidia of *I. neglectus* have a posteroaxis that always is longer than the anteroaxis and the stout node reaches behind the F2 furrow. F1 crosses the axis, with laterally deep impressions. *Agnostus neglectus* thus shows differences to both *Agnostus* and *Homagnostus* and it was assigned to *Innitagnostus* by Öpik (1967) and Rushton (1978) and we concur with that allocation.

Family Ptychagnostidae Kobayashi, 1939

Genus *Acidusus* Öpik, 1979

Type species (OD). – *Ptychagnostus* (*Acidusus*) *acidusus* Öpik, 1979, from the V-Creek Limestone (*Doryagnostus notalibrae* Zone) of Queensland, Australia.

Diagnosis. – See Öpik (1979) and Shergold & Laurie (1997).

Remarks. – Several authors consider *Acidusus* as a junior synonym of *Ptychagnostus* (e.g. Peng & Robison 2000). Three species, *A. aculeatus* (Angelin, 1851), *A. atavus* (Tullberg, 1880) and, questionably, *A.*? *cassis* Öpik, 1961, occur in the Miaolingian of Scandinavia.

Acidusus aculeatus **(Angelin, 1851)**

Figure 15A–O

1851 *Agnostus aculeatus* n. sp. Angelin, p. 8, pl. 6, fig. 12.
1878 *Agnostus aculeatus* Angelin; Brøgger, p. 71, pl. 5, fig. 5.
1880 *Agnostus aculeatus* Angelin; Tullberg, p. 23, pl. 1, fig. 11a, b.
1902 *Agnostus aculeatus* Angelin; Grönwall, p. 197.
1929 *Agnostus aculeatus* Angelin; Strand, p. 345, pl. 1, fig. 7.
1946 *Ptychagnostus* (*Ptychagnostus*) *aculeatus* (Angelin); Westergård, p. 79, pl. 12, figs 8–11.
1961 *Ptychagnostus* (*Ptychagnostus*) *aculeatus* (Angelin); Öpik, p. 80, pl. 21, figs 3, 4.
1962 *Ptychagnostus aculeatus* (Angelin); Lu, p. 29, pl. 3, figs 7, 10.
1963 *Ptychagnostus aculeatus* Angelin; Egorova, Xiang, Li, Nan & Guo, p. 63, pl. 7, figs 6, 7.
1964 *Ptychagnostus aculeatus* (Angelin); Lu, p. 28, pl. 2, figs 10, 11.
1965 *Ptychagnostus aculeatus* (Angelin); Lu, Zhang, Zhu, Qian & Xiang, p. 37, pl. 3, figs 11, 12.
1968 *Ptychagnostus* (*Ptychagnostus*) *aculeatus* (Angelin); Palmer, p. 28, pl. 6, fig. 20.
1970 *Ptychagnostus aculeatus* (Angelin); Hajrullina, p. 7, pl. 1, figs 4, 5.
1973 *Ptychagnostus aculeatus* (Angelin); Hajrullina, p. 34, pl. 1, figs 5–7.
1976 *Ptychagnostus* (*Ptychagnostus*) cf. *aculeatus* (Angelin); Jago, p. 152, pl. 23, fig. 12.
1981 *Ptychagnostus* (*Ptychagnostus*) *aculeatus* (Angelin); Zhang, p. 137, pl. 55, figs 1, 2.
1982 *Ptychagnostus aculeatus* (Angelin); Kindle, pl. 1.2, figs 16, 19, 23.
1982 *Ptychagnostus* (*Ptychagnostus*) *aculeatus*; Yang, pl. 1, figs 16, 17.
1984 *Ptychagnostus aculeatus* (Angelin); Robison, p. 14, fig. 8.
1985 *Ptychagnostus aculeatus* (Angelin); Xiang & Zhang, p. 73, pl. 21, fig. 1.
1988 *Acidusus aculeatus* (Angelin); Laurie, p. 186.
1989 *Ptychagnostus aculeatus* (Angelin); Lu & Lin, pp. 95, 216, pl. 8, figs 1–3.
1991 *Ptychagnostus aculeatus* (Angelin); Yang *et al.*, p. 106, pl. 2, fig. 5.
1992 *Ptychagnostus aculeatus* (Angelin); Jago & Webers, p. 107, pl. 1, fig. 17.
1994 *Ptychagnostus aculeatus* (Angelin); Bordonaro & Liñán, p. 112, pl. 2, figs 7–9.
1994 *Ptychagnostus aculeatus* (Angelin); Rudolph, p. 111, pl. 4, figs 13–14, 17–18.
1995 *Ptychagnostus aculeatus* (Angelin); Bordonaro & Banchig, pl. 1, fig. 7.
1996 *Ptychagnostus aculeatus* (Angelin); Cooper, Jago & Begg, p. 370, fig. 5N.
1996 *Ptychagnostus aculeatus* (Angelin); Westrop, Ludvigsen & Kindle, p. 816, fig. 15.5.
1996 *Ptychagnostus aculeatus* (Angelin); Zhou, Cao, Hu & Zhao, pl. 6, figs 1, 2.
1997 *Ptychagnostus aculeatus* (Angelin); Tortello & Bordonaro, p. 79, fig. 3:27, 28.
1997 *Goniagnostus* (*Allobodochus*) *aculeatus* (Angelin); Jell & Hughes, p. 88, pl. 28, figs 3, 4.
2000 *Ptychagnostus aculeatus* (Angelin); Peng & Robison, p. 68, fig. 50.
2008 *Goniagnostus aculeatus* (Angelin); Høyberget & Bruton, p. 55, pl. 9, figs M–P.
2008 *Ptychagnostus aculeatus* (Angelin); Ergaliev & Ergaliev, p. 99, pl. 12, figs 1–5.
2009a *Ptychagnostus aculeatus* (Angelin); Peng *et al.*, fig. 9K, L.
2009b *Ptychagnostus aculeatus* (Angelin); Peng *et al.*, figs 13, 15:8, 9.
2011 *Acidusus aculeatus* (Angelin); Jago, Bentley & Cooper, p. 23, fig. 4J–O.
2014 *Acidusus aculeatus* (Angelin); Bentley & Jago, p. 271, fig. 3E.

Lectotype (designated by Westergård 1946). – Cephalon, NRM Ar1997a, figured by Westergård (1946, pl. 12, fig. 8) from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – About 20 cephala and pygidia of *A. aculeatus* were collected at Siljeåsen, Högnäsån, Långseleån and Fjällbränna. Other occurrences in the study area are at Fånån and Abborrfallet (Asklund & Thorslund 1935). The specimens are associated with typical representatives of the lower part of the *L. laevigata* Zone, viz. *H. brevifrons*, *C. confusus*, *L. kjerulfi*, *M. glandiformis* and three species of *Proampyx*. Westergård (1946) reported *A. aculeatus* from the Swedish provinces Scania, Västergötland, Jämtland and Ångermanland; it also occurs in southern Norway (Høyberget & Bruton 2008) and on Bornholm, Denmark (Grönwall 1902). In the Krekling section, Norway, *A. aculeatus* appears already in the *G. nathorsti* Zone (Brøgger 1878). It has also been found in ice-rafted boulders of the Exporrecta Conglomerate Bed at As Hoved, Denmark (collection TW) and in northern Germany (Rudolph 1994), in both cases with provenance from Västergötland. Outside Scandinavia, it occurs in Argentina (Bordonaro & Liñán 1994), Antarctica (Cooper *et al.* 1996; Jago *et al.* 2011), Australia (Öpik 1961; Bentley & Jago 2014), Kazakhstan (Ergaliev & Ergaliev 2008), the Turkestan range (Hajrullina 1970, 1973), Indian Himalaya (Jell & Hughes 1997; Peng

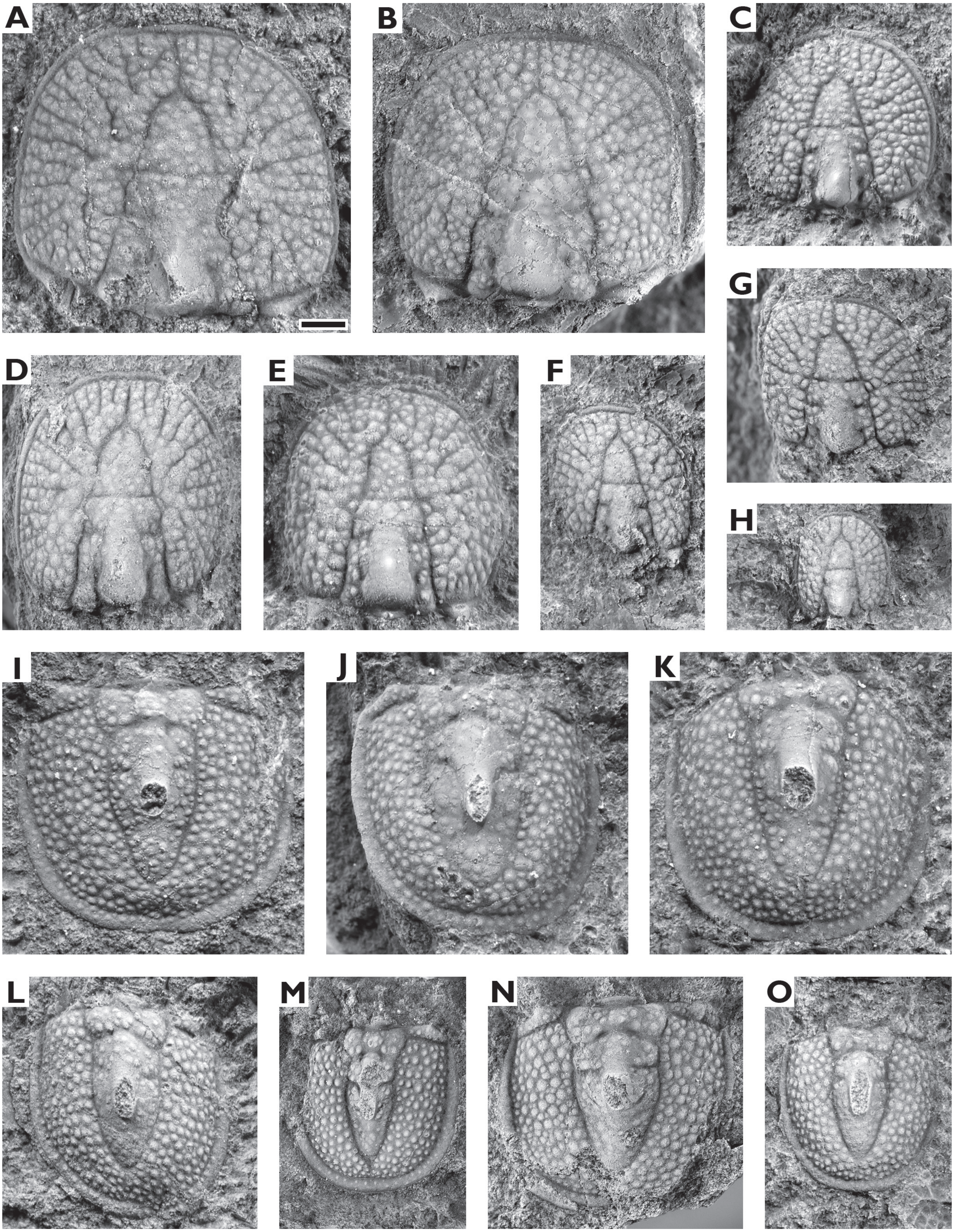


Fig. 15. ***Acidusus aculeatus*** **(Angelin, 1851)**, lower part of the *L. laevigata* Zone. **A**–**H**, cephala. PMU 37127b/2, 37130, 37127a/1, 37129/2, 37127b/3, 37129/3, 37129/1, 37129/4. **I**–**O**, pygidia. PMU 37124–37126, 37128/1, 26248, 26189, 37129/5. A–K, O are from Långseleån, L is from Fjällbränna, M from Högnäsån and N from Siljeåsen. Scale bar = 1 mm.

et al. 2009b), China (Peng & Robison 2000), the Great Basin, USA (Robison 1984), Alaska (Palmer 1968) and Laurentian Canada (Kindle 1982). The species is everywhere infrequent to rare and all reports are from the lower part of the *L. laevigata* Zone.

Remarks. – For descriptions of the species, see Westergård (1946) and Robison (1984). *Acidusus aculeatus* is easy to recognize due to its generally large size and the coarse surface granulation of both shields. The cephala possess posterolateral spines, but most of the illustrated specimens in the cited references are fragmentary or the spines are broken off, precluding precise assessment of the length of the spines. A few Scandinavian specimens show short or intermediate spines (Westergård 1946, pl. 12, fig. 11; Høyberget & Bruton 2008, pl. 9, fig. M); figured cephala from China also have intermediate spines (Peng & Robison 2000, fig. 50:1, 2) whereas those from USA illustrated by Robison (1984, fig. 8:1, 7) have long spines, approaching the length of the cephalon. The width of the spine base is not proportional to the length of the spine. Høyberget & Bruton (2008) regarded the material from the Great Basin, USA, as a different species, but as the cephala and pygidia otherwise show no differences, we retain them as *A. aculeatus*.

Our specimens match the material described from Scania (Westergård 1946) and Norway (Høyberget & Bruton 2008). Some of the cephala have a coarser surface granulation and the radiating scrobicules appear less distinct and are in places even replaced by granulation, thereby resembling the cephalon from China illustrated by Peng & Robison (2000, fig. 50:1). Fully grown cephala and pygidia of *P. punctuosus* are smaller than *A. aculeatus*, have a finer surface granulation and the pygidial axis lacks the prominent spine.

***Acidusus atavus* (Tullberg, 1880)**

Figure 16A–R

1880 *Agnostus atavus* n. sp. Tullberg, p. 14, pl. 1, figs 1a–d.
1946 *Ptychagnostus* (*Ptychagnostus*) *atavus* (Tullberg); Westergård, p. 76, pl. 11, figs 8–25.
1962 *Ptychagnostus atavus* (Tullberg); Hutchinson, p. 83, pl. 8, figs 16–22; pl. 9, figs 1–8.
1979 *Ptychagnostus atavus* (Tullberg); Öpik, p. 93, pl. 29, fig. 7; pl. 42, figs 7–8; pl. 43, figs 1–4; textfig. 27.
pars 1982 *Ptychagnostus atavus* (Tullberg); Egorova *et al*., p. 63, pl. 6, fig. 7; pl. 7, fig. 6; pl. 11, figs 1–3; pl. 13, fig. 13; pl. 55, figs 16, 18, 20–21; *non* pl. 51, fig. 11 [= *T. gibbus* (Linnarsson, 1869)].
1984 *Ptychagnostus atavus* (Tullberg); Robison, p. 18, fig. 11.
2000 *Ptychagnostus atavus* (Tullberg); Peng & Robison, p. 69, fig. 52.
2008 *Ptychagnostus atavus* (Tullberg); Høyberget & Bruton, p. 49, pl. 7, figs G–M.
2012 *Acidusus atavus* (Tullberg); Buchholz, pl. 1, figs A–F; pl. 2, figs D, L.
2014 *Acidusus atavus* (Tullberg); Weidner & Nielsen, p. 32 (*cum syn.*), figs 9, 10A–D, 11A–H, 12F–H.

Lectotype (designated by Westergård 1946). – Cephalon, LO 354t, originally figured by Tullberg (1880, pl. 1, fig. 1a, c) and later by Westergård (1946, pl. 11, fig. 8). It derives from the lower part of the *A. atavus* Zone in the Alum Shale Formation at Andrarum, Scania, Sweden.

Material and occurrence. – *Acidusus atavus* occurs abundantly at Långseleån, Fjällbränna and Djupdalsbäcken and, less commonly, at Högnäsån, Karbäcken and Tåsjö church on the Tåsjö Mountain. It is widely distributed and has been reported from the *A. atavus* Zone or strata of similar age from Sweden (Westergård 1946), Denmark (Weidner & Nielsen 2014), Norway (Høyberget & Bruton 2008), ice-rafted boulders of northern Germany (Mischnik 2006c), maritime Canada (Hutchinson 1962), Laurentian Canada (Kindle 1982), Greenland (Robison 1994), USA (Robison 1984; Palmer 1968), Australia (Öpik 1979), China (Peng & Robison 2000), Russia (Egorova *et al.* 1982) and Kazakhstan (Ergaliev & Ergaliev 2008).

Remarks. – For detailed descriptions of the species and remarks on differences from *Ptychagnostus affinis*, we refer to Westergård (1946), Robison (1984), Laurie (1988) and Weidner & Nielsen (2009, 2014). Our specimens display variations in the cephalon, having a nearly smooth surface or scrobiculation of variable intensity, including a pair of arcuate furrows, and also in the pygidium, having a lanceolate or ogival posteroaxix and a median postaxial furrow present or absent.

Genus *Goniagnostus* Howell, 1935c

Type species (OD). – *Agnostus nathorsti* Brøgger, 1878, from the *G. nathorsti* Zone, Alum Shale Formation at Krekling, Oslo Region, Norway.

Diagnosis. – See Laurie (1989), Shergold & Laurie (1997) and Peng & Robison (2000).

Remarks. – Two species, *G.* (*Goniagnostus*) *nathorsti* (Brøgger, 1878) and *G.* (*Allobodochus*) *spiniger* (Westergård, 1931), occur in the Miaolingian of Scandinavia. Additionally, material from Norway may represent *G. scarabaeus* Whitehouse, 1939 (Høyberget & Bruton 2008).

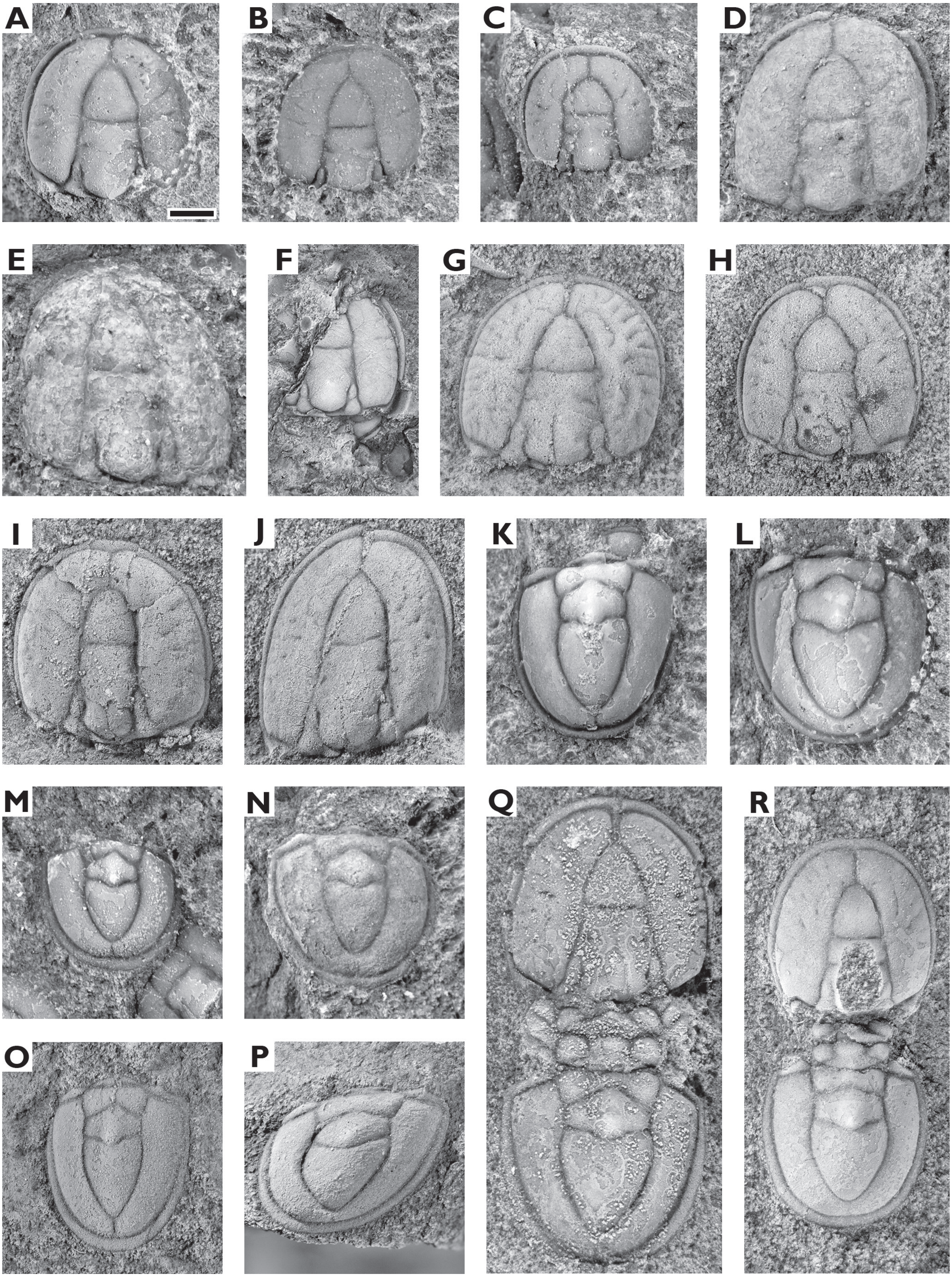


Fig. 16. ***Acidusus atavus*** **(Tullberg, 1880)**, *A. atavus* Zone. **A**–**J**, cephala. PMU 37080, 37082/1, 37082/2, 37086/1, 37086/2, 23062/1, 26114/2, 26114/3, 26116/3, 26117/2. **K**–**P**, pygidia. PMU 37084/2, 37081, 37082/3, 37089/3, 26117/1, 26115/2. **Q**–**R**, complete specimens. PMU 31863, 26104. A–C and K–M are from Djupdalsbäcken, D–E and N are from Fjällbränna, F is from Långseleån showing the distinct elongate and divided basal lobes. G–J and O–R are from Tåsjö church. Note the pair of arcuate furrows in G. Scale bar = 1 mm.

Goniagnostus (*Goniagnostus*) *nathorsti* (Brøgger, 1878)

Figure 17A–V

1878 *Agnostus nathorsti* n. sp. Brøgger, p. 68, pl. 5, fig. 1.
1880 *Agnostus nathorsti* Brögger; Tullberg, p. 21, pl. 1, fig. 9.
1902 *Agnostus nathorsti* Brögger; Grönwall, p. 54.
1929 *Agnostus nathorsti* Brøgger; Strand, p. 345.
1935c *Goniagnostus nathorsti* (Brögger); Howell, p. 13, figs 1, 2 [*Goniagnostus* erected].
1946 *Goniagnostus nathorsti* (Brögger); Westergård, p. 81, pl. 12, figs 12–16.
1960 *Goniagnostus nathorsti* (Brögger); Poletaeva *in* Khalfina, p. 159, pl. 18, fig. 2a–b.
1967 *Goniagnostus nathorsti* (Brögger); Hucke & Voigt, p. 49, pl. 6, fig. 6.
1970 *Goniagnostus nathorsti* (Brögger); Hajrullina, p. 8, pl. 1, figs 6–9.
1973 *Goniagnostus nathorsti* (Brögger); Hajrullina, p. 36, pl. 1, figs 8–13.
1977 *Goniagnostus nathorsti* (Brögger); Fedjanina, p. 146, pl. 19, figs 5, 6.
1979 *Goniagnostus nathorsti* (Brögger); Neben & Krueger, pl. 115, figs 7, 8.
1979 *Goniagnostus nathorsti* (Brögger); Öpik, p. 150, pl. 60, figs 1–5; pl. 61, figs 1, 3–6; textfig. 48.
1980 *Goniagnostus nathorsti* (Brögger); Ergaliev, p. 73, pl. 2, figs 1, 2.
1982 *Goniagnostus nathorsti* (Brögger); Egorova *et al*., p. 66, pl. 17, figs 2–4; pl. 18, fig. 6; pl. 21, fig. 2; pl. 44, fig. 1.
1985 *Goniagnostus nathorsti* (Brögger); Xiang & Zhang, p. 74, pl. 20, figs 1–3, 6–10.
1988 *Goniagnostus nathorsti* (Brögger); Lisogor, Rozov & Rozova, p. 60, pl. 4, figs 5–6.
1989 *Goniagnostus* (*Goniagnostus*) *nathorsti* (Brögger); Laurie, p. 177, fig. 1.
1990 *Goniagnostus* (*Goniagnostus*) *nathorsti* (Brögger); Shergold, Laurie & Sun, p. 76, fig. 11:6.
1994 *Goniagnostus nathorsti* (Brögger); Rudolph, p. 118, pl. 6, figs 8–11.
1997 *Goniagnostus* (*Goniagnostus*) *nathorsti* (Brögger); Shergold & Laurie, p. 350, fig. 223:3a–c.
1999 *Goniagnostus* (*Goniagnostus*) *nathorsti* (Brøgger); Bruton, p. 337, fig. 1.
2000 *Goniagnostus nathorsti* (Brögger); Pegel, fig. 11:12.
2000 *Goniagnostus nathorsti* (Brøgger); Peng & Robison, p. 72, fig. 56.
2001 *Goniagnostus nathorsti* (Brøgger); Jago & Brown, p. 2, pl. 1, figs A–K.
2003 *Goniagnostus nathorsti* (Brøgger); Axheimer & Ahlberg, p. 145, fig. 4L–M.
2004 *Goniagnostus nathorsti* (Brögger); Weidner, Ahlberg, Axheimer & Clarkson, fig. 3N–S.
2008 *Goniagnostus nathorsti* (Brøgger); Høyberget & Bruton, p. 54, pl. 9, figs F, G.
2008 *Goniagnostus nathorsti* (Brögger); Ergaliev & Ergaliev, p. 108, pl. 7, figs 11–16; pl. 12, figs 8, 9, 12.
2009 *Goniagnostus nathorsti*; Ahlberg *et al*., fig. 3M–N.
2009a *Goniagnostus nathorsti* (Brøgger); Peng *et al*., fig. 9M–N.
2011 *Goniagnostus nathorsti* (Brøgger); Jago, Bentley & Cooper, p. 23, fig. 5A–H.
2016 *Goniagnostus nathorsti* (Brögger); Pegel, Egorova, Salikhova & Shabanov, p. 28, pl. 9, fig. 18.
2016 *Goniagnostus nathorsti* (Brögger); Makarova & Bushuev, pl. 2, figs 10, 11.

Neotype (designated by Bruton 1999). – Internal mould of a complete specimen, PMO 19887, figured by Shergold & Laurie (1997, fig. 223:3a) and Bruton (1999, fig. 1A). The specimen is preserved in shale from the *G. nathorsti* Zone at Krekling, Oslo Region, Norway.

Material and occurrence. – In the study area, the species is common in the eponymous zone at Siljeåsen, Abborrfallet, Sågbäcken, Fjällbränna and Skansholm. It is further reported from the Tåsjö church locality by Asklund & Thorslund (1935) and from the Skikkisjö Mountain by Kulling (1955). Elsewhere in Sweden, *G. nathorsti* is known also from Scania, Västergötland (Westergård 1946; Weidner *et al*. 2004) and a few more localities in Jämtland and Ångermanland (Westergård 1946). The species is reported also from Norway (Høyberget & Bruton 2008) and Bornholm, Denmark (Grönwall 1902). *Goniagnostus nathorsti* is most common in the eponymous zone but occurs sparsely also in the lower part of the *L. laevigata* Zone (Westergård 1946). Asklund & Thorslund (1935) described a block with an unusual assemblage from Siljeåsen, containing *G. nathorsti*, *P. punctuosus*, *Glaberagnostus*? *cicer* and *L. laevigata*. From ice-rafted boulders of northern Germany, the species is known from the *G. nathorsti* Zone and the Andraum Limestone Bed (Rudolph 1994). Outside Scandinavia, it has been reported from Australia (Öpik 1979), where it is rare in the *P. punctuosus* Zone and common in the *G. nathorsti* Zone, from the ?lower part of the *L. laevigata* Zone of Antarctica (Jago *et al*. 2011), from the *G. nathorsti* Zone of China (Peng & Robison 2000), the *P. punctuosus* and the *G. nathorsti* zones of Kazakhstan (Ergaliev & Ergaliev 2008), from the Turkestan range (Hajrullina 1970, 1973), from the *G. nathorsti* and the lower part of the *L. laevigata* zones of Siberia (Egorova *et al*. 1982) and from the *G. nathorsti* Zone of Avalonian Canada at New Brunswick (Matthew 1896).

Remarks. – Öpik (1979) and Laurie (1989) gave a detailed account of *G.* (*G.*) *nathorsti* including remarks on its distinction from similar species in Scandinavia. Our new material complies with illustrations of material from Sweden (Westergård 1946), Norway (Høyberget & Bruton 2008), China (Peng & Robison 2000) and Australia (Laurie 1989). The only other safely assigned species of *Goniagnostus* occurring in Scandinavia, *Goniagnostus spiniger* from the upper part of the *L. laevigata* Zone, has long posterior cephalic and pygidial spines and a distinctive granular ornament, which is especially visible on the pleural fields of the pygidium (Laurie 1989, fig. 6; Peng & Robison 2000, fig. 59).

Pygidia of *G. nathorsti* resemble those of *Doryagnostus incertus* from the *P. punctuosus* Zone in having a depressed posteroaxis. However, *G. nathorsti* has a segmented axis with a long spinose node, the

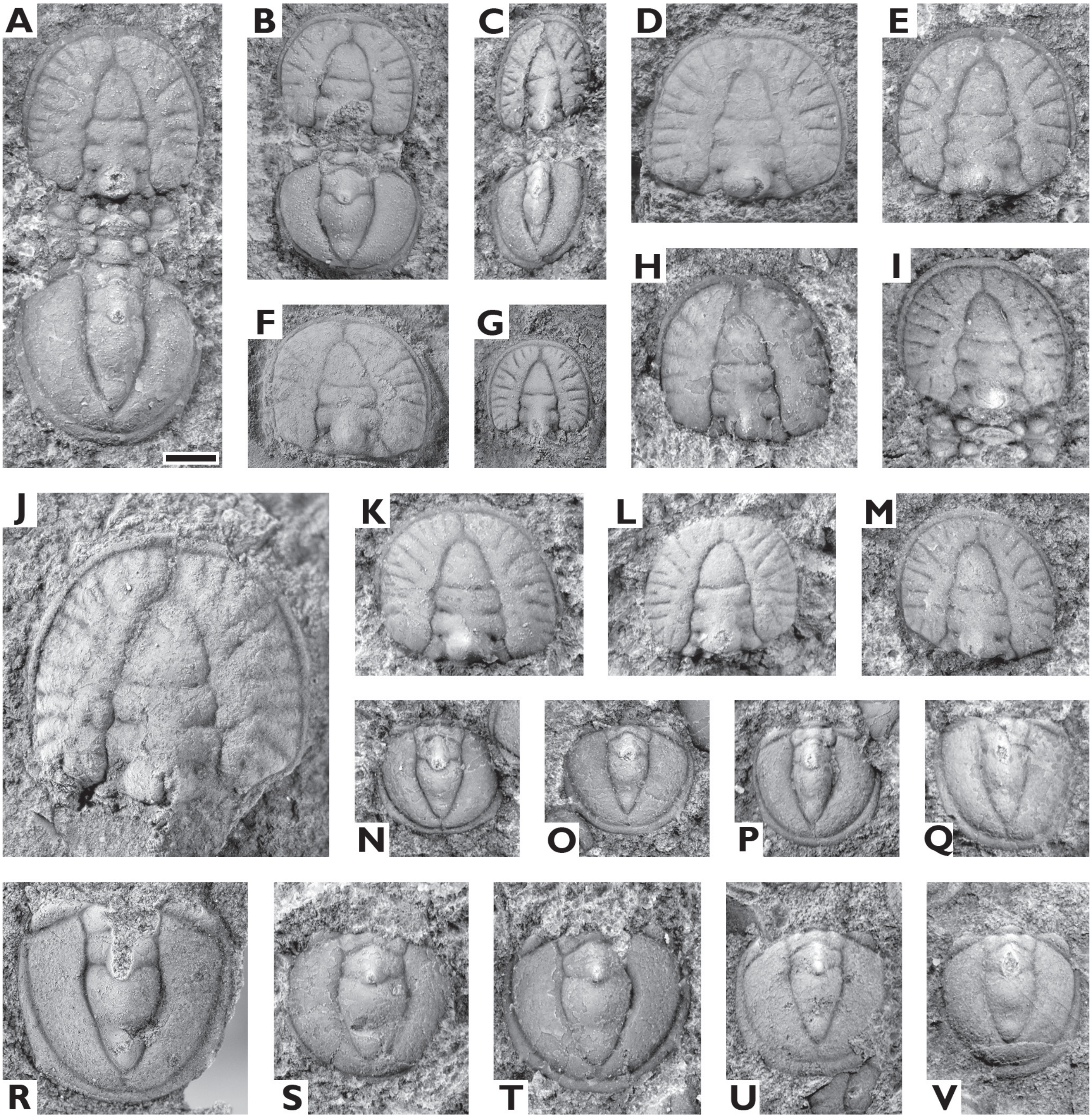


Fig. 17. ***Goniagnostus (Goniagnostus) nathorsti*** **(Brøgger, 1878)**, *G. nathorsti* Zone. **A–C**, complete specimens. PMU 37097/1, 37101/1, 37101/2. **D–M**, cephala. PMU 37100, 37099, 29692/1, 26573/6, 37094/1, 37092, 26282, 37093/1, 37093/2, 37098, **N–V**, pygidia. PMU 37094/3, 37094/4, 37094/2, 37093/3, 26573/1, 37095/1, 37095/2, 37091/3, 37090. A–E, H–I, K–Q and S–T are from Skansholm, F and U–V are from Fjällbränna, G and R are from Abborrfallet and J is from Brattbäcken. Scale bar = 1 mm.

latter has an unsegmented axis, faint or no constrictions at F1, and a distinct but smaller axial node.

Genus *Lejopyge* Hawle & Corda, 1847

Type species (OD). – *Battus laevigatus* Dalman, 1828, from the *L. laevigata* Zone, Alum Shale Formation on Mount Kinnekulle, Västergötland, Sweden.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Five species, *L. laevigata* (Dalman, 1828), *L. armata* (Linnarsson, 1869), *L. elegans* (Tullberg, 1880), *L. lundgreni* (Tullberg, 1880) and *L. calva* Robison, 1964, are known from the Miaolingian of Scandinavia.

Lejopyge calva **Robison, 1964**

Figure 18A–G, I–K, M–Q

pars 1902 *Agnostus laevigatus* Dalman; Grönwall, p. 60.
1964 *Lejopyge calva* n. sp. Robison, p. 521, pl. 83, figs 1–4.
1968 *Lejopyge calva* Robison; Palmer, p. 27, pl. 6, figs 15–18.
1975 *Lejopyge exilis* Whitehouse; Daily & Jago, pl. 63, fig. 11.
1979 *Lejopyge praecox* sp. nov. Öpik, p. 159, pl. 66, figs 1–7.
1980 *Lejopyge calva* Robison; Ergaliev, p. 79, pl. 2, fig. 12.
1984 *Lejopyge calva* Robison; Robison, p. 40, fig. 23.
1989 *Lejopyge calva* Robison; Laurie, p. 189.
1994 *Lejopyge calva* Robison; Robison, p. 52, fig. 24.
1996 *Lejopyge calva* Robison; Cooper, Jago & Begg, p. 370, fig. 5H, I.
2000 *Lejopyge calva* Robison; Peng & Robison, p. 78, fig. 62.
2008 *Lejopyge laevigata* (Dalman); Ergaliev & Ergaliev, pl. 11, figs 3, 4.
2008 *Lejopyge calva* Robison; Høyberget & Bruton, p. 59, pl. 10, figs P–W.
2009 *Lejopyge laevigata*; Ahlberg *et al*., fig. 3A, ?B, C.
2009a *Lejopyge calva* Robison; Peng *et al*., fig. 9E–G.
2011 *Lejopyge calva* Robison; Jago, Bentley & Cooper, p. 21, fig. 3E–I.

Holotype (OD). – Cephalon, USNM 141227a, illustrated by Robison (1964, pl. 83, fig. 1) from the *L. calva* Subzone, uppermost division of the *Bolaspidella* Zone in Utah, USA. It was refigured by Daily & Jago (1975, pl. 63, fig. 10).

Material and occurrence. – *Lejopyge calva* is common at Fjällbränna and Strömnäs and rare at Abborrfallet. About 100 cephala and pygidia have been collected. It is associated with *G. nathorsti*, *L. lundgreni*, *A. ferox*, *D. planicauda bilobatus*, *T. exsculpta* and *V. marginatus*. In Scandinavia, these species all range at least through the *G. nathorsti* Zone and the lower part of the *L. laevigata* Zone. In Norway, *L. calva* is common at two localities where it occurs with the same association of agnostoids (Høyberget & Bruton 2008). This is the first report of *L. calva* from Sweden. However, one cephalon and one pygidium from just below the Andrarum Limestone Bed in the Andrarum–3 core that were figured as *L. laevigata* by Ahlberg *et al*. (2009) are considered by us to represent *L. calva*. From Bornholm, Denmark, a few specimens of *L. calva* from the *Davidis* Zone were listed as *L. laevigata* by Grönwall (1902), see remarks below. The species is common in Laurentia (USA with Alaska, and Greenland) (Robison 1964, 1984, 1994; Palmer 1968) and Gondwana (Australia, Antarctica) (Daily & Jago 1975; Öpik 1979; Jago *et al*. 2011). It also occurs in China (Peng & Robison 2000) and Kazakhstan (Ergaliev 1980). Globally, it ranges from the *P. punctuosus* Zone to the lower part of the *L. laevigata* Zone.

Remarks. – *Lejopyge calva* is generally non-spinose but specimens from Norway and Antarctica may show minute cephalic and pygidial spines. The cephalon varies between being circular to more elongate in outline, with a narrow border and glabellar furrows completely effaced, except along the most posterior part of the posteroglabella. An incipient median preglabellar furrow is visible in some cephala. A faint glabellar node is usually seen at 3/10 of the cephalic length from the rear. The pygidium is rounded posteriorly with a border considerably wider than in the cephalon, and widening posteriorly. Pygidial furrows are very faint adjacent to M1, otherwise effaced. The M2 node is indistinct. Our specimens comply with all these key features; all pygidia are non-spinose.

Lejopyge calva differs from the younger *L. laevigata* in having more effaced axial furrows and a wider pygidial border (see Fig. 18G versus H, and 18K versus L).

Grönwall (1902, pp. 60, 198) reported *L. laevigata* from the *Davidis* Zone of Bornholm, which comprises the *P. punctuosus* and *G. nathorsti* zones, and from the lower part of the *L. laevigata* Zone. The older specimens, associated with *G. nathorsti* and *D. planicauda bilobatus*, were described as 'not completely typical'. One cephalon and one pygidium from the collection of the Natural History Museum of Denmark, University of Copenhagen (sample GM 2020.1), were investigated by us. They represent *L. calva*.

Lejopyge cf. *L. laevigata* (Axheimer & Ahlberg 2003, p. 145, fig. 4N) from the Almbacken core in Scania was considered to represent a pygidium of *L. calva* by Høyberget & Bruton (2008). The specimen has a wide border as in *L. calva*, but unlike the latter, the axial furrows are faintly outlined. It is not associated with any of the agnostoids of the typical fauna accompanying *L. calva* in Västerbotten and Norway, and we question the proposed assignment.

Lejopyge elegans **(Tullberg, 1880)**

Figure 19A–H

1880 *Agnostus elegans* n. sp. Tullberg, p. 19, pl. 1, fig. 7a–d.
1902 *Agnostus elegans* Tullberg; Grönwall, p. 57.
1946 *Ptychagnostus* (*Triplagnostus*) *elegans* (Tullberg); Westergård, p. 74, pl. 10, figs 11–20.
1946 *Ptychagnostus* (*Triplagnostus*) *elegans laevissimus* subsp. n. Westergård, p. 74, pl. 10, figs 21, 22.
1984 *Lejopyge elegans* (Tullberg); Robison, p. 37.
1994 *Lejopyge elegans* (Tullberg); Rudolph, p. 122, pl. 5, figs 2–7.
non 2002 *Lejopyge elegans* (Tullberg); Rushton & Berg-Madsen, fig. 2p, q [= *Cotalagnostus claudicans* Westergård, 1946].
2004 *Lejopyge elegans* (Tullberg); Weidner, Ahlberg, Axheimer & Clarkson, fig. 3F–H.
2008 *Lejopyge elegans* (Tullberg); Høyberget & Bruton, p. 60, pl. 10, figs A–C.

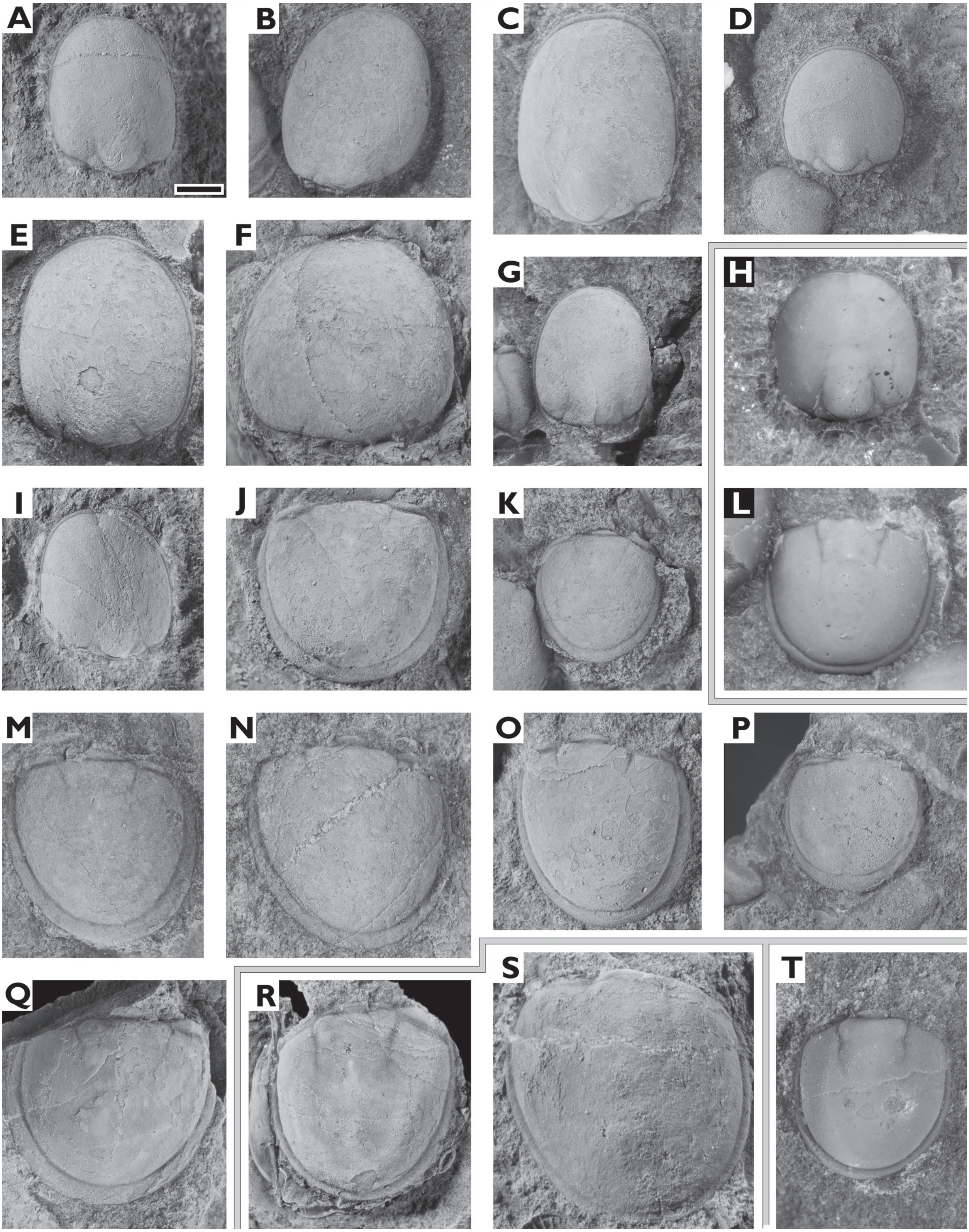


Fig. 18. ***Lejopyge calva*** **Robison, 1964**, *G. nathorsti* Zone. **A**, **C**–**D**, **I**, cephala, Abborrfallet. PMU 26597/3, 26576/1, 26573/5, 26597/4. **B**, **E**–**G**, cephala, Fjällbränna. PMU 29691/10, 29690/1, 29692/5, 29690/2. **Q**, pygidium, Abborrfallet, 26605/3. **J**–**K**, **M**–**P**, pygidia, Fjällbränna. PMU 29691/5, 29691/4, 29692/4, 29689, 29691/1, 29688. ***Lejopyge laevigata*** **(Dalman, 1828), H**, cephalon and **L**, pygidium, both with faintly outlined axial lobes to compare vs *L. calva*, upper part of *L. laevigata* Zone, ice-rafted boulder, As Hoved, Denmark. MGUH 34031–34032. **R**, pygidium, Långseleån and **S**, pygidium, Fjällbränna, both from the lower part of the *L. laevigata* Zone. PMU 29710, 36427/1. ***Lejopyge*** **cf.** ***laevigata***. **T,** pygidium of from Lubbträsk, collected by E. Mörtzell. SGU 9877. Scale bar = 1 mm.

Lectotype (designated by Westergård 1946). – Cephalon, LO 368t, from the *P. punctuosus* Zone at Andrarum (Tullberg's locality 11), Scania, Sweden. It was figured by Westergård (1946, pl. 10, fig. 11).

Material and occurrence. – Only 2 cephala and 6 pygidia were collected from the *P. punctuosus* Zone at Strömnäs and Granberget. It is an infrequent to rare species, known only from Scandinavia. In Sweden, is has been described from Västergötland (Weidner *et al.* 2004) and Scania (Westergård 1946). It has also been found in ice-rafted boulders at As Hoved, Denmark, with provenance from Västergötland (collection TW), on Bornholm, Denmark, (Grönwall 1902) and at one locality in Norway (Høyberget & Bruton 2008). All reports are from the *P. punctuosus* Zone.

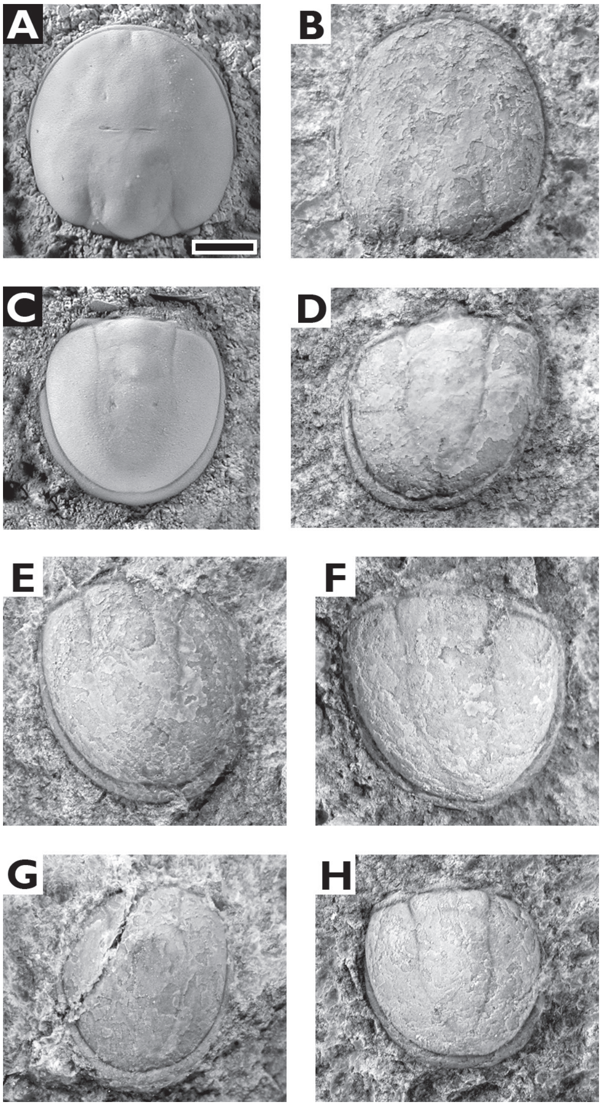


Fig. 19. ***Lejopyge elegans*** (**Tullberg, 1880**), *P. punctuosus* Zone. **A**–**B**, cephala. LO 9552t, PMU 37107, **C**–**H**, pygidia. LO 9554t, PMU 37104, 37105, 37102, 37106, 37103. A, C, specimens from Vilske, Västergötland, showing well the diagnostic features, for comparison. Both have been previously illustrated by Weidner *et al.* (2004, Figs 3F and 3H). B, D–H are all from Granberget. Scale bar = 1 mm.

Remarks. – We fully agree with the description of the species provided by Høyberget & Bruton (2008); for good illustrations, see Westergård (1946) and Weidner *et al.* (2004). In *L. elegans*, the cephalic and pygidial furrows and the nodes are faint and the cephalic border is very narrow. In the closely related species *L. lundgreni*, all furrows are fully developed and the nodes are distinct. For comparison of the two species, see Weidner *et al.* (2004, fig. 3F–H versus 3J–M) and Figure 20.

Rushton & Berg-Madsen (2002) refigured the pygidium illustrated as *A. lens* by Cobbold & Pocock (1934, pl. 44, fig. 7) and hesitantly assigned it to *L. elegans*. The specimen has a broad, flat border, widening posteriorly, distinct axial furrows, a strong axial node, constricted M2 and a distinct median postaxial furrow, all features typical of *C. claudicans* (Fig. 28U). The pygidium of *L. elegans* has a narrow border and faint axial and transaxial furrows and a small, faint node (cf. Westergård 1946, pl. 10, figs 12, 14, 16, 19; Weidner *et al.* 2004, fig. 3G–H; Fig. 19).

Lejopyge laevigata (Dalman, 1828)

Figure 18H, L, R, S

1828 *Battus laevigatus* Dalman, p. 136.
1837 *Battus laevigatus* Dalman; Hisinger, p. 20, pl. 4, fig. 7.
1847 *Lejopyge laevigata* (Dalman); Hawle & Corda, p. 51, pl. 3, fig. 25.
1851 *Agnostus lævigatus* Dalman; Angelin, p. 6, pl. 6, fig. 3.
1869 *Agnostus laevigatus* Dalman; Linnarsson, p. 82.
1873 *Agnostus laevigatus* Dalman; Linnarsson, p. 246.
1876 *Agnostus laevigatus* Dalman; Brøgger, p. 194, pl. 8, fig. 1.
1878 *Agnostus laevigatus* Dalman; Brøgger, p. 74, pl. 5, fig. 6.
1880 *Agnostus laevigatus* Dalman; Tullberg, p. 27, pl. 2, fig. 17a, b.
1885 *Agnostus laevigatus* Dalman; Roemer, p. 31, pl. 1, fig. 5a–d.
1896 *Agnostus laevigatus* Dalman; Koken, p. 347, fig. 242:3.
1896 *Agnostus laevigatus* Dalman; Wallerius, pp. 165–170.
pars 1902 *Agnostus laevigatus* Dalman; Grönwall, p. 60.
1929 *Agnostus laevigatus* Dalman; Strand, p. 346.
1946 *Lejopyge laevigata* (Dalman); Westergård, p. 87, pl. 13, figs 18–27; pl. 16, fig. 9.
1946 *Lejopyge laevigata armata* (Linnarsson); Westergård, p. 89, pl. 13, figs 30, 31.
1946 *Lejopyge laevigata rugifera* subsp. n. Westergård, p. 90, pl. 14, fig. 3.
1958 *Lejopyge laevigata* (Dalman); Pokrovskaya, p. 76, pl. 5, figs 16–17.
1960 *Lejopyge laevigata* (Dalman); Poletaeva *in* Khalfina, p. 163, pl. 18, fig. 3a, b.

1961 *Leiopyge laevigata* (Dalman); Öpik, p. 85, pl. 21, figs 5–9.
1967 *Lejopyge laevigata* (Dalman); Hucke & Voigt, p. 49, pl. 5, fig. 6.
1967 *Leiopyge cos* sp. nov. Öpik, p. 93, pl. 57, figs 5, 6.
1968 *Lejopyge laevigata* (Dalman); Palmer, p. 28, pl. 6, fig. 19.
?1970 *Lejopyge laevigata* (Dalman); Hajrullina, p. 16, pl. 1, fig. 15.
1971 *Lejopyge laevigata* (Dalman); Hill, Playford & Woods, p. 20, pl. 10, figs 5, 6.
?1973 *Lejopyge laevigata* (Dalman); Hajrullina, p. 50, pl. 3, figs 11–14.
1975 *Lejopyge laevigata* (Dalman); Daily & Jago, p. 527, pl. 62, figs 1–10.
1975 *Lejopyge laevigata rugifera* (Westergård); Daily & Jago, p. 529, pl. 63, fig. 6.
1975 *Lejopyge laevigata armata* (Linnarsson); Daily & Jago, p. 528, pl. 62, figs 15, 16.
1975 *Lejopyge cos* Öpik; Daily & Jago, p. 528, pl. 62, figs 17, 18.
?1975 *Lejopyge laevigata* (Dalman); V. Poulsen & Anderson, p. 2075, pl. 2, figs 1–9 [= indet.].
1976 ?*Lejopyge laevigata* (Dalman); Jago, p. 12, pl. 2, fig. 1, 2.
1979 *Lejopyge laevigata* (Dalman); Neben & Krueger, pl. 115, fig. 9; pl. 117, figs 3–5.
1979 *Leiopyge laevigata* (Dalman); Öpik, p. 161, pl. 64, figs 1–3.
1980 *Lejopyge laevigata* (Dalman); Ergaliev, p. 77, pl. 3, figs 1–9.
1981 *Lejopyge laevigata* (Dalman); Zhang: 139, pl. 55, fig. 6.
?1982 *Lejopyge laevigata* (Dalman); Egorova *et al.*, p. 74, ?pl. 25, fig. 1; ?pl. 28, figs 2–5; ?pl. 46, fig. 6.
1984 *Lejopyge laevigata* (Dalman); Robison, p. 42, fig. 25.
1988 *Lejopyge laevigata* (Dalman); Robison, p. 49, fig. 12:2, 3.
1989 *Lejopyge laevigata* (Dalman); Laurie, p. 188, fig. 8.
pars 1989 *Lejopyge laevigata* (Dalman); Lu & Lin, pp. 104, 221, pl. 10, fig. 15; *non* figs 13,14 [= *L. armata* (Linnarsson, 1869)].
1990 *Lejopyge laevigata* (Dalman); Dong, pl. 3, figs 7, 8.
1990 *Lejopyge laevigata* (Dalman); Shergold, Laurie & Sun, fig. 11:5.
1991 *Lejopyge laevigata* (Dalman); Dong, pl. 3, figs 2, 5.
1991 *Lejopyge laevigata* (Dalman); Yang *et al.*, p. 106, pl. 2, figs 6, 7.
1994 *Lejopyge laevigata* (Dalman); Rudolph, p. 119, pl. 5, figs 10–13, ?14, 15, 16, ?17, 18, 19.
1997 *Lejopyge laevigata* (Dalman); Shergold & Laurie, fig. 224:5a, b.
1997 *Lejopyge laevigata* (Dalman); Tortello & Bordonaro, p. 79, fig. 4:3–6.
2000 *Lejopyge laevigata* (Dalman); Pegel, fig. 11:9.
2000 *Lejopyge laevigata* (Dalman); Peng & Robison, p. 76, fig. 60.
2001 *Lejopyge laevigata* (Dalman); Jago & Brown, p. 5, pl. 1L, M, P–S; 2C.
?2003 *Lejopyge* cf. *laevigata* (Dalman); Axheimer & Ahlberg, p. 145, fig. 4N.
2006 *Lejopyge laevigata* (Dalman); Axheimer, Eriksson, Ahlberg & Bengtsson, p. 452, fig. 6a, b.
pars 2008 *Lejopyge laevigata* (Dalman); Ergaliev & Ergaliev, p. 111, pl. 11, *non* figs 3, 4 [= *Lejopyge calva* Robison, 1964]; pl. 17, figs 1, ?2, 3–7, ?8, 9, 10.
2008 *Lejopyge calva* Robison; Ergaliev & Ergaliev, pl. 11, figs 18–20.
2008 *Lejopyge laevigata* (Dalman); Høyberget & Bruton, p. 57, pl. 10, figs H, K–M, O.
2008 *Lejopyge armata* (Linnarsson); Høyberget & Bruton, p. 58, pl. 10, fig. N.
2009a *Lejopyge laevigata* (Dalman); Peng *et al.*, fig. 9H–J.
2010 *Lejopyge laevigata* (Dalman); Buchholz, pl. 2, fig. 10.
2014 *Lejopyge laevigata* (Dalman); Bentley & Jago, pl. 271, fig. 3F.
2016 *Lejopyge laevigata* (Dalman); Pegel, Egorova, Salikhova & Shabanov, p. 29, pl. 9, figs 11, 15.

Lectotype (designated by Westergård 1946). – Cephalon, NRM Ar287b, illustrated by Westergård (1946, pl. 13, fig. 21) and re-illustrated by Shergold *et al.* (1990, fig. 5A) and Shergold & Laurie (1997, fig. 224:5b). The latter authors also choose a paralectotype pygdium, NRM Ar287a (Shergold & Laurie 1997, fig. 224:5a). The type specimens derive from the *L. laevigata* Zone at Hönsäter, Kinnekulle, Västergötland.

Material and occurrence. – Limestone from this level is very scarce in the study area. One pygidium was found at Långseleån and one at Fjällbränna, associated with *A. aculeatus*, *C. confusus*, *L. kjerulfi* and *M. glandiformis*, clearly indicative of the lower part of the *L. laevigata* Zone. Asklund & Thorslund (1935) reported *L. laevigata* from Fånån and Abborrfallet. Greiling & Grimmer (2014) cited Gee (1972) for an occurrence of *L. laevigata* at Stalon. The main collection at SGU houses one pygidium of *Lejopyge* cf. *laevigata* from Lubbträsk (Fig. 18T). The undeformed pygidium differs from *laevigata* in M2 being as wide as M1; in *laevigata* M1 is always wider than M2. *Lejopyge laevigata* often occurs in great abundance in Sweden (Westergård 1946), Norway (Høyberget & Bruton 2008) and Denmark (Grönwall 1902) in the upper part of the eponymous zone and it has been recorded also from ice-rafted boulders found in Denmark (collection TW) and northern Germany (Rudolph 1994). Elsewhere, the species occurs in the *L. laevigata* Zone of Siberia (Pokrovskaya 1958), Kazakhstan (Ergaliev 1980), the Turkestan range (Hajrullina 1970, 1973), China (Peng & Robison 2000), Australia (Öpik 1961; Daily & Jago 1975; Jago & Brown 2001), Argentina (Tortello & Bordonaro 1997), Alaska (Palmer 1968) and Greenland (Robison 1984, 1988).

For remarks on *L. laevigata* reported from the *Davidis* Zone of Bornholm by Grönwall (1902), see *L. calva*.

Remarks. – The pygidia at hand have a narrow border of even width and with axial furrows distinctly developed slightly behind the axial node, which are typical traits of *L. laevigata*. *Lejopyge calva* has a wide border, widening posteriorly, and the axial furrows do not extend to the axial node. *Lejopyge armata* has distinct marginal spines.

Cephala of *L. laevigata* with scrobiculate surface were treated by Westergård (1946) as the subspecies

L. laevigata rugifera. However, having smooth, weakly or strongly scrobiculate cheeks is a variable character in Ptychagnostidae (Robison 1982) and is known from several middle Cambrian species, e.g. *Acidusus atavus*, *Onymagnostus hybridus*, *Pentagnostus praecurrens*, *Tomagnostus fissus*, *Tomagnostus sibiricus*, *Tomagnostella exsculpta* and *Triplagnostus gibbus* (cf. Weidner & Nielsen 2014, 2015b; Weidner & Ebbestad 2014; Westergård 1946). This feature is generally no longer used as a taxonomic character and we consider *L. laevigata rugifera* as a junior synonym. Laurie (1989) assigned pygidia with minute marginal spines to *L. laevigata* rather than *L. armata*, which is accepted by most authors (Tortello & Bordonaro 1997; Peng & Robison 2000; Axheimer *et al*. 2006).

Lejopyge lundgreni (Tullberg, 1880)

Figure 20A–R

1880 *Agnostus Lundgreni* n. sp. Tullberg, p. 20, pl. 1, fig. 8a, b.
1902 *Agnostus Lundgreni* Tullberg; Grönwall, p. 51.
1902 *Agnostus Lundgreni*, var. nana, n. var. Grönwall, p. 51, pl. 1, fig. 2.
1929 *Agnostus atavus* Tullberg; Strand, p. 344, pl. 1, fig. 20.
1929 *Agnostus lundgreni nana* Grönwall; Strand, p. 345, pl. 1, figs 5, 6.
1934 *Agnostus lundgreni* Tullberg; Cobbold & Pocock, p. 342, pl. 44, fig. 20, ?21.
1946 *Ptychagnostus* (*Triplagnostus*) *lundgreni* (Tullberg); Westergård, p. 75, pl. 10, figs 23–25; pl. 11, figs 1, 2.
1946 *Ptychagnostus* (*Triplagnostus*) *lundgreni nanus* (Grönwall); Westergård, p. 75, pl. 11, figs 3–7.
1979 *Ptychagnostus* (*Triplagnostus*) *lundgreni* (Tullberg); Neben & Krueger, pl. 115, fig. 11.
1982 *Triplagnostus lundgreni* (Tullberg); Egorova *et al*., p. 65. pl. 54, fig. 16.
1984 *Lejopyge lundgreni* (Tullberg); Robison, p. 46, figs 27, 28.
non 1994 *Lejopyge lundgreni* (Tullberg); Rudolph, p. 123, pl. 5, fig. 1 [= *A. atavus* (Tullberg 1880)].
2000 *Pseudophalacroma lundgreni* (Tullberg); Peng & Robison, p. 81, fig. 66.
2003 *Ptychagnostus lundgreni* (Tullberg); Axheimer & Ahlberg, p. 147, fig. 5H.
2003 *Ptychagnostus lundgreni* forma *nanus* (Grönwall); Axheimer & Ahlberg, p. 147, fig. 5I.
2004 *Ptychagnostus lundgreni* (Tullberg); Weidner, Ahlberg, Axheimer & Clarkson, fig. 3J–M.
2008 *Lejopyge lundgreni* (Tullberg); Høyberget & Bruton, p. 61, pl. 9, figs Q–V.
pars 2009 *Ptychagnostus lundgreni*; Ahlberg *et al*., fig. 3P, *non* O [= indet.].

Lectotype (designated by Westergård 1946). – Cephalon, LO 370t, figured by Westergård (1946, pl. 10, fig. 23) from the *P. punctuosus* Zone at Øleå, Borggård, Bornholm, Denmark.

Material and occurrence. – *Lejopyge lundgreni* has been collected from the *P. punctuosus* Zone at Kvarnbäcken and Strömnäs and at the latter locality and Fjällbränna also from the overlying *G. nathorsti* Zone. At Fjällbränna, the species is quite common. Elsewhere in Sweden, it is reported from Scania, where it ranges into the lower part of the *L. laevigata* Zone, Västergötland, Jämtland and Ångermanland (Westergård 1946; Weidner *et al.* 2004). It has been recorded also from Bornholm, Denmark (Tullberg, 1880; Grönwall 1902) and southern Norway (Høyberget & Bruton 2008) and it is common in ice-rafted boulders at As Hoved, Denmark, with provenance from Västergötland (Weidner *et al.* 2004). Other reports are from England (Cobbold & Pocock 1934), Siberia (Egorova *et al.* 1982), USA (Robison 1984) and China (Peng & Robison 2000). It generally ranges from the *P. punctuosus* Zone into the lower part of the *L. laevigata* Zone.

Remarks. – The species has been illustrated and described in detail by Robison (1984) from the Great Basin, USA, and by Høyberget & Bruton (2008) from Norway. Our new specimens match entirely the diagnostic features. The axial furrows vary in the degree they are bowed outwards at M2 in the cephalon and in the posteroaxis in the pygidium. The surface of the cheeks may be either smooth or furrowed.

Genus *Onymagnostus* Öpik, 1979

Type species (OD). – *Onymagnostus angulatus* Öpik, 1979, from the Currant Bush Limestone (*P. punctuosus* Zone) of Queensland, Australia. This species is a junior synonym of *Agnostus gibbus*, var. *hybrida*, Brøgger, 1878 from the *P. punctuosus* Zone at Krekling, Norway (e.g. Shergold & Laurie 1997; Høyberget & Bruton 2008).

Diagnosis. – See Öpik (1979) and Shergold & Laurie (1997).

Remarks. – Four species, *O. hybridus* (Brøgger, 1878), *O. ciceroides* (Matthew, 1896), *O. seminula* (Whitehouse, 1939) and *O. mundus* (Öpik, 1979) are recorded from the Miaolingian of Scandinavia.

Onymagnostus hybridus (Brøgger, 1878)

Figures 21A–Q, 34H (cephalon only), I–J

1878 *Agnostus gibbus*, var. *hybrid* Brøgger, p. 62, pl. 5, figs 4a, b.
1902 *Agnostus stenorrhachis* n. sp. Grönwall, p. 76, pl. 1, fig. 16.
1916 *Agnostus pulchellus* sp. nov. Illing, p. 410, pl. 30, figs 1–2.

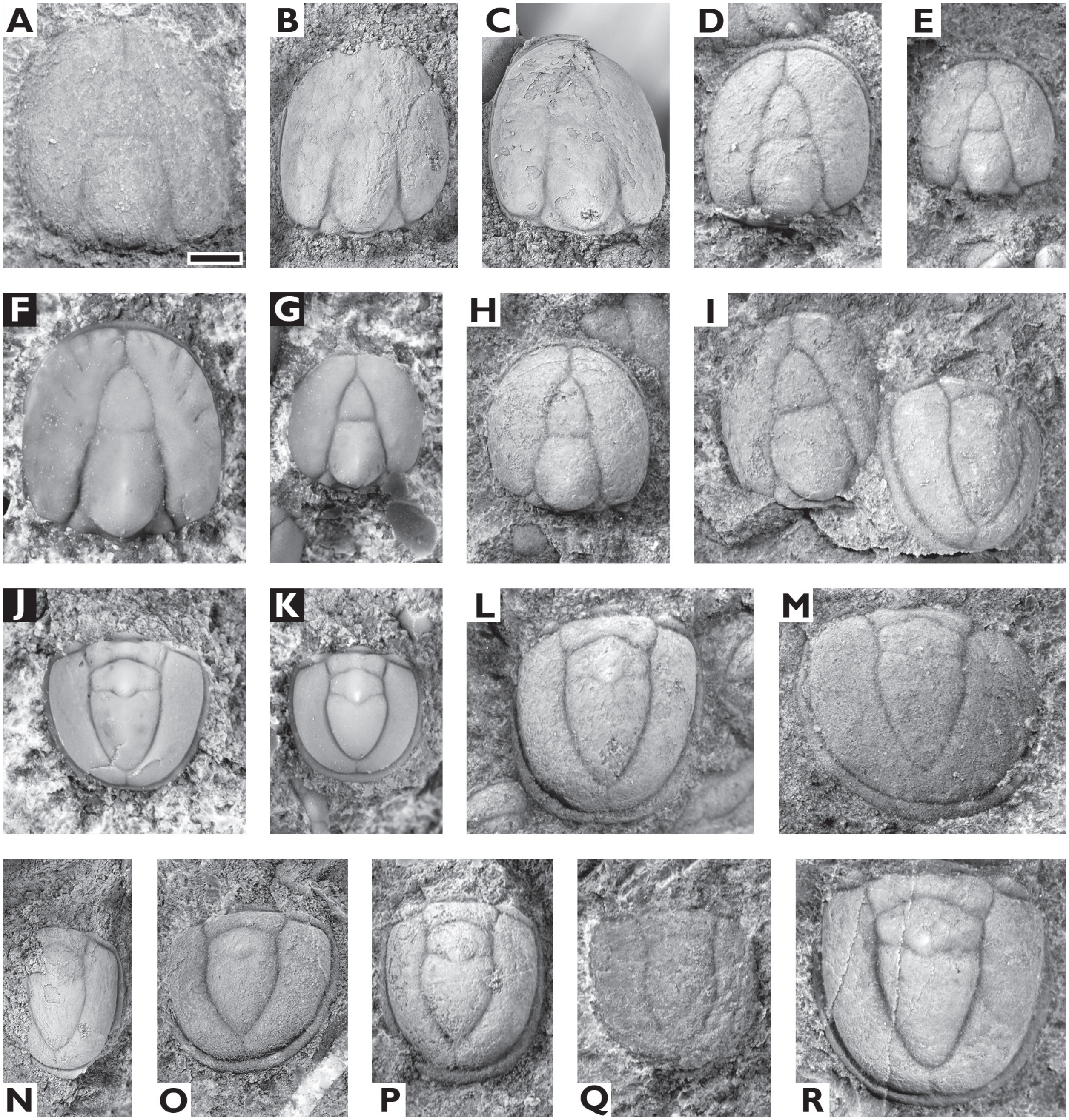


Fig. 20. ***Lejopyge lundgreni*** **(Tullberg, 1880)**. **A–I**, cephala. A, *P. punctuosus* Zone, Strömnäs. PMU 37110. B–C, *P. punctuosus* Zone, Kvarnbäcken. PMU 26237/2, 26237/3. D–E, *G. nathorsti* Zone, Fjällbränna. PMU 37113/3, 37113/1. F–G, well-preserved specimens from ice-rafted boulders at As Hoved, Denmark, for comparison. *P. punctuosus* Zone. MGUH 34033–34034. H–I (left specimen), *G. nathorsti* Zone, Fjällbränna. PMU 37113/4, 37112/1. **I–R**, pygidia. I (right specimen), *G. nathorsti* Zone, Fjällbränna. PMU 37112/2. J–K, well-preserved specimens from ice-rafted boulders at As Hoved, Denmark, for comparison. *P. punctuosus* Zone. MGUH 34035–34036. L, O–P, R, *G. nathorsti* Zone, Fjällbränna. PMU 37113/5, 37115, 37113/2, 37091/1. M, Q, *P. punctuosus* Zone, Strömnäs. PMU 37114, 37111. N, *P. punctuosus* Zone, Kvarnbäcken. PMU 26237/4. Scale bar = 1 mm.

non 1934 *Agnostus stenorrhachis* Grönwall; Cobbold & Pocock, p. 342, pl. 44, fig. 22 [= indet.].

1946 *Ptychagnostus* (*Triplagnostus*) *hybridus* (Brögger); Westergård, p. 71, pl. 9, figs 25, 26; pl. 10, figs 1–2.

1946 *Ptychagnostus* (*Triplagnostus*) *stenorrhachis* (Grönwall); Westergård, p. 72, pl. 10, figs 3, 4.

1962 *Ptychagnostus* (*Triplagnostus*) *stenorrhachis* (Groenwall); Hutchinson, p. 80, pl. 8, figs 1–5.

1977 *Ptychagnostus* (*Ptychagnostus*) *stenorrhachis* (Grönwall); Jago, p. 45, pl. 1, figs 7–12.

1979 *Ptychagnostus* (*Triplagnostus*) *hybridus* (Brögger); Neben & Krueger, pl. 115, figs 5, 6.

pars 1982 *Triplagnostus stenorrhachis* (Grönwall); Egorova *et al.*, p. 65, pl. 11, figs 9, 10; pl. 12, figs 7–9; pl. 13, figs 4, 5, 7; pl. 14, figs 1–3; pl. 15, figs 2, 3; pl. 18, figs 2, 3; pl. 21, fig. 4; pl. 22, figs 8, 9; pl. 61, figs 1, 2; *non* pl. 19, fig. 1 [= indet.].

1997 *Onymagnostus hybridus* (Brögger); Shergold & Laurie, pp. 352, 354, fig. 224:2a, b.
2006 *Ptychagnostus hybridus* (Brögger); Fletcher, p. 86.
2011 *Onymagnostus hybridus* (Brøgger); Jago, Bentley & Cooper, p. 21, fig. 4A–I.
2012 *Onymagnostus hybridus* (Brøgger); Buchholz, pl. 2, figs M–O.
2014 *Onymagnostus hybridus* (Brøgger); Weidner & Nielsen, p. 38 (*cum syn.*), fig. 16.

Lectotype (designated by Shergold & Laurie 1997). – Pygidium, PMO 28096, originally illustrated by Brøgger (1878, pl. 5, fig. 4b) and refigured by Shergold & Laurie (1997, fig. 224:2b). It derives from the *P. punctuosus* Zone in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Material and occurrence. – *Onymagnostus hybridus* is common in the *A. atavus* Zone at Fjällbränna and Granberget and it was also found in this zone at Högnäsån on the Tåsjö Mountain. The species is known from the same stratigraphic level in many Swedish provinces (Westergård 1946), Norway (Høyberget & Bruton 2008), Great Britain (Thomas *et al.* 1984), Bohemia (Vaněk & Valíček 2001), Siberia (Egorova *et al.* 1982), Canada (Westrop *et al.* 1996; Fletcher 2006), Greenland (Robison 1994) and Australia (Öpik 1979; Laurie 1988). It also occurs in the overlying *P. punctuosus* Zone on Bornholm, Denmark (Grönwall 1902), in Sweden (Westergård 1946), Norway (Høyberget & Bruton 2008), Canada (Hutchinson 1962), Australia (Jago 1977) and USA (Robison 1984) and in the lower part of the *L. laevigata* Zone of Antarctica (Jago *et al.* 2011).

Comparison. – *Onymagnostus hybridus* is characterized by a cephalon with rounded anteroglabella provided with a minute mesial point, a slightly expanded M2 lobe, laterally faintly indicated F1 and F2 and smooth or occasionally scrobiculate cheeks. The cheeks narrow considerably forward, often to half the posterior width. The pygidium has a long axis, which is approximately as wide as a pleural field, M1 is undivided or tripartite, and M2 carries a stout node strongly deflecting F2 (Weidner & Nielsen 2014, fig. 16). The most notable intraspecific variation is the width of the

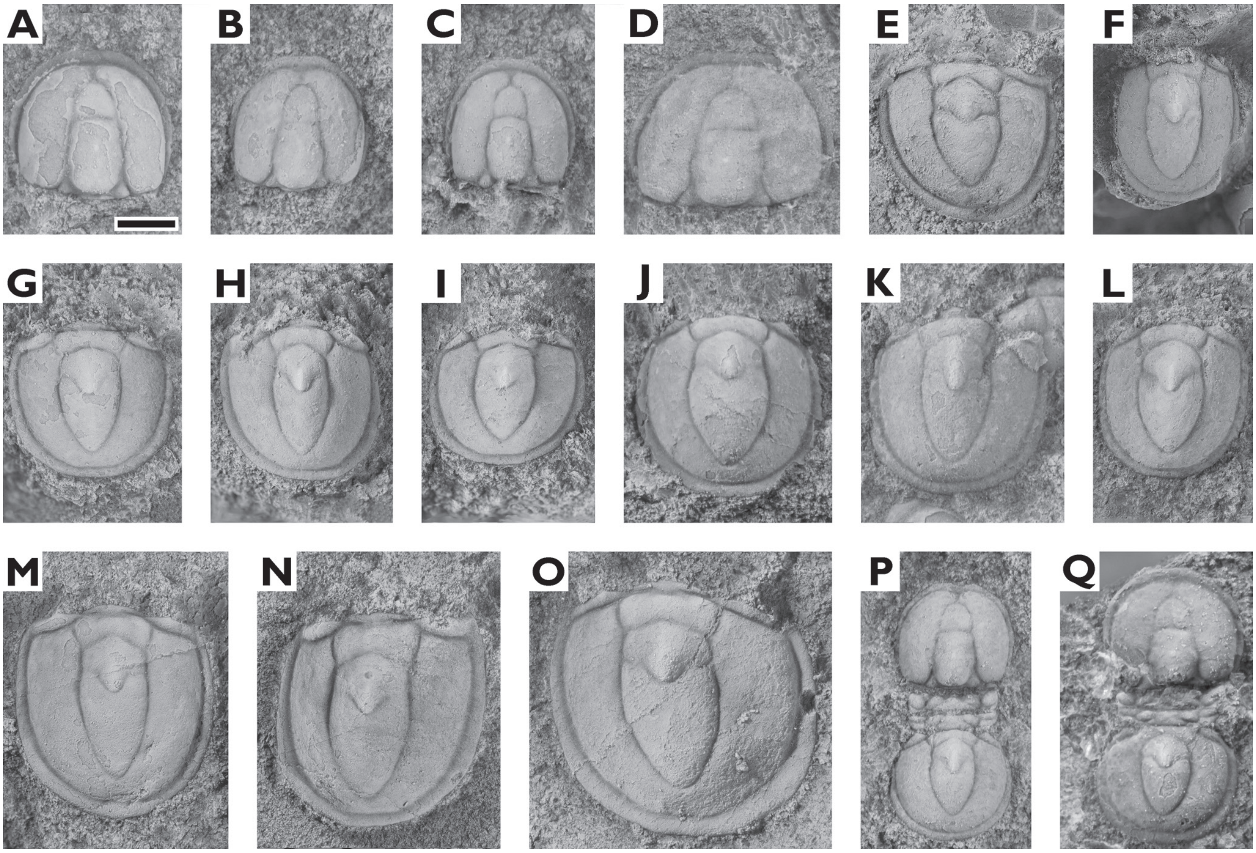


Fig. 21. **Onymagnostus hybridus (Brøgger, 1878)**, *A. atavus* Zone. **A**–**D**, cephala. PMU 37119, 37118, 37120, 37122. **E**–**O**, pygidia. PMU 26169/2, 29693/3, 29694/1, 29705/2, 29703/4, 37121, 37117, 29705/3, 26169/1, 26171, 26168. **P**–**Q**, complete specimens. PMU 37116, 37123. A–C, F–L and P–Q are from Granberget. D is from Fjällbränna. E and M–O are from Högnäsån. Scale bar = 1 mm.

pygidial axis (see Høyberget & Bruton 2008, pl. 11, figs A–E).

The new cephala from Lapland have a wider median preglabellar furrow than seen in illustrated material from Norway (Bruton 1999), Sweden (Westergård 1946; Weidner & Nielsen 2009), Bornholm (Weidner & Nielsen 2014) and USA (Robison 1984), but otherwise agree. For remarks on the variability of the pygidia, see discussion below.

Cephala of *O. hybridus* are difficult to distinguish from those of *D. incertus*. In *O. hybridus*, the greatest cephalic width is behind the transglabellar furrow, in *D. incertus* it is at level with the transglabellar furrow or anterior of it. Another difference is the expanded M2 in *O. hybridus*, while M2 is more slender and parallel-sided in *D. incertus*. The pygidial differences between the two species are, however, unmistakable. *Onymagnostus hybridus* is characteristic for the upper part of the *A. atavus* Zone and *D. incertus* for the *P. punctuosus* Zone, but in some regions the two species may overlap in the latter zone.

Discussion. – Robison (1984) synonymized *O. stenorrhachis* (Grönwall, 1902) with *O. hybridus* and this interpretation was adopted also by Jago *et al.* (2011). Grönwall (1902), who had only pygidia of *O. stenorrhachis* at hand, emphasized the axial outline being long and strongly pointed and narrower than the pleural field. It can be added that M1 is distinctly tripartite in this original specimen. The principal differences between *O. stenorrhachis* and *O. hybridus* are according to Westergård (1946) the smooth cheeks in *O. hybridus* versus pits and irregular scrobicules in the cheeks of *O. stenorrhachis* and a much narrower pygidial axis in the latter. The pygidium figured by Westergård (1946, pl. 10, fig. 4) has an axis slightly wider and less pointed than in the specimen described by Grönwall (1902) and M1 displays a faint tripartition. Hutchinson (1962) reported *O. stenorrhachis* from the *P. punctuosus* Zone of eastern Newfoundland (Avalonian Canada). He observed that all cephala show a pair of short indistinct furrows in front of the anteroglabella. This feature is also faintly indicated in Westergård's specimen (1946, pl. 10, fig. 3). Jago *et al.* (2011, pp. 21–23, fig. 4A–I) figured cephala and pygidia from Antarctica (as *O. hybridus*) that show all the diagnostic features of *O. stenorrhachis*, i.e. pitted and grooved cheeks, short indistinct furrows anterior of the anteroglabella, a sharply pointed axis considerably narrower than a pleural field, and a distinct tripartition of M1. Because of these apparent differences in both cephala and pygidia we were originally reluctant to synonymize *O. hybridus* and *O. stenorrhachis* (Weidner & Nielsen 2014), but based on a renewed review of figured material of these species we conclude:

(1) A varied scrobiculation of the cheeks within the same species is a recurrent phenomenon in many species and should be treated with caution as a taxonomic character, see for instance *Pentagnostus praecurrens*, *Triplagnostus gibbus*, *Tomagnostus sibiricus*, *Acidusus atavus*, *Hypagnostus frontosa*, *Tomagnostella exsculpta*, '*Diplorrhina*' *cylindrica* and *Lejopyge lundgreni* (Westergård 1946; Weidner & Ebbestad 2014; Weidner & Nielsen 2014, 2015b).

(2) Arcuate furrows in agnostoids are commonly situated laterally of the anteroglabella. Having a pair of very faint furrows placed in front of the anteroglabella is an unusual feature that can be seen also in holaspid cephala of *O. hybridus* (Robison 1984, fig. 30:5b; Weidner & Nielsen 2014, fig. 16A, F).

(3) The width of the pygidial axis seems to vary considerably in *O. hybridus* (see Shergold & Laurie 1997, fig. 224:2b; Høyberget & Bruton 2008, pl. 11, figs A, C; Weidner & Nielsen 2009, fig. 11C). The pygidium of *O. stenorrhachis* illustrated by Westergård (1946, pl. 10, fig. 4) can hardly be distinguished from the pygidium of *O. hybridus* illustrated by Høyberget & Bruton (2008, pl. 11, fig. A). We now interpret pygidia with a very narrow axis as figured by Grönwall (1902) and Hutchinson (1962) and those with a very wide axis (Høyberget & Bruton 2008; Weidner & Nielsen 2009) as two extremes of the same species.

(4) The tip of the pygidial axis in *O. hybridus* is normally gently rounded, but pygidia with a sharply pointed axis, just like in figured specimens of *O. stenorrhachis*, occur as well (Buchholz 2012, pl. 2, fig. M).

(5) M1 in the pygidia of *O. hybridus* is generally undivided, whereas in specimens attributed to *O. stenorrhachis* the M1 is tripartite (Grönwall 1902; Jago *et al.* 2011). However, this feature can also be found in *O. hybridus* (cf. Høyberget & Bruton 2008, pl. 11, fig. E).

Our review shows that all features assumed diagnostic of *O. stenorrhachis*, with particular emphasis on the unique pair of furrows placed in front of the anteroglabella, can be observed also in material assigned to *O. hybridus* and we now concur with Robison (1984) and Jago *et al.* (2011) that *O. stenorrhachis* should be treated as junior synonym of *O. hybridus*.

Genus *Pentagnostus* Lermontova, 1940

Type species (OD). – *Pentagnostus anabarensis* Lermontova, 1940, from the *T. gibbus* Zone at Anabar River, Republic of Yakutia, Russia.

Diagnosis. – See Robison (1982) and Shergold & Laurie (1997).

Remarks. – *Pentagnostus praecurrens* (Westergård, 1936) is the only representative of this genus reported from the Miaolingian of Scandinavia. Some authors assign *praecurrens* to *Ptychagnostus* (Robison 1984 a.o.) or *Triplagnostus* (Korovnikov & Shabanov 2016).

Pentagnostus praecurrens (Westergård, 1936)

Figure 22A–M

1936 *Agnostus gibbus* Linnarsson *praecurrens* n. var. Westergård, p. 29, pl. 1, figs 19–23.
2009 *Pentagnostus praecurrens* (Westergård); Laurie, p. 687, fig. 1.
2014 *Pentagnostus praecurrens* (Westergård); Weidner & Ebbestad, p. 403, figs 4–10.
2014 *Pentagnostus praecurrens* (Westergard); Danukalova, Kuzmichev & Korovnikov, p. 361, pl. 2, fig. 5.
2015b *Pentagnostus praecurrens* (Westergård); Weidner & Nielsen, p. 16 (*cum syn.*), fig. 12D–F.
2016 *Pentagnostus praecurrens* (Westergård); Pegel, Egorova, Salikhova & Shabanov, p. 30, pl. 9, figs 9, 10.
2016 *Triplagnostus praecurrens* (Westergård); Korovnikov & Shabanov, pl. 2, fig. 14a–c.

Holotype (OD). – Cephalon, SGU 611, originally illustrated by Westergård (1936, pl. 1, fig. 19), collected from the Mossberga core, Öland, Sweden. It derives from the *A. pinus* – *P. praecurrens* Zone. Refigured by Laurie (2009, fig. 1A) and Weidner & Ebbestad (2014, fig. 4A).

Material and occurrence. – *Pentagnostus praecurrens* is common in the eponymous zone at Rökbergsbäcken and Marbäcken on the Tåsjö Mountain, in Stendalsbäcken near Djupdal and at the shore of Storvindeln near Hemfjäll (see also Weidner & Ebbestad 2014). The species is known also from various localities in central Jämtland, Närke, Östergötland and Öland (Weidner & Ebbestad 2014 and references therein). Three specimens have been found in the Exsulans Limestone Bed in Scania, representing the *T. gibbus* Zone (Weidner & Nielsen 2015b, fig. 12D, E). Outside Sweden, the species occurs in the *P. praecurrens* Zone in England, British Columbia (Canada), and Australia. In Siberia, Russia, it occurs in strata contemporaneous with the *A. pinus* – *P. praecurrens* and *T. gibbus* zones and it may even range into the lower part of the *A. atavus* Zone. For references, see Weidner & Ebbestad (2014).

Remarks. – In spite of considerable tectonic deformation of the specimens from Hemfjäll, most of the diagnostic features can still be recognized. The cephala have a narrow border delimited by a deep and narrow border furrow (Fig. 22A, D, E), the median glabellar furrow is either present or absent (Fig. 22B, D, E), F3 is medially slightly bent backwards and F2 is laterally distinct. The best preserved pygidia show an almost straight F2 furrow (Fig. 22H, J), no median postaxial furrow and a narrow border delimited by a narrow and deep border furrow. Juvenile specimens from Stendalsbäcken were treated by Weidner & Ebbestad (2014).

Genus *Ptychagnostus* Jaekel, 1909

Type species (OD). – *Agnostus punctuosus* Angelin, 1851, from a stinkstone lens in the *P. punctuosus* Zone, Alum Shale Formation at Andrarum, Scania, Sweden.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – For remarks on genus, see Westergård (1946), Peng & Robison (2000) and Ahlberg *et al.* (2007). All of these authors adopted a broader concept of the genus than Shergold & Laurie (1997) and herein. Two species, *P. punctuosus* (Angelin, 1851) and *P. affinis* (Brøgger, 1878), are known from the Miaolingian of Scandinavia according to the restricted concept of the genus accepted here.

Ptychagnostus affinis (Brøgger, 1878)

Figure 23A–N

1878 *Agnostus punctuosus*, Ang. var. *affinis* Brøgger, p. 68, pl. 5, figs 2a, b.
1946 *Ptychagnostus* (*Ptychagnostus*) *punctuosus affinis* (Brøgger); Westergård, p. 79, pl. 11, figs 26–33.
1979 *Ptychagnostus punctuosus affinis* (Brøgger); Öpik, p. 91, pl. 39, fig. 8; pl. 40, figs 2–7.
1984 *Ptychagnostus affinis* (Brøgger); Robison, p. 16, fig. 9.
1988 *Ptychagnostus affinis* (Brøgger); Laurie, p. 172, fig. 2A–E.
2000 *Ptychagnostus affinis* (Brøgger); Peng & Robison, p. 68, fig. 51.
?2008 *Ptychagnostus affinis* (Brögger); Ergaliev & Ergaliev, p. 99, pl. 2, figs 14, 15.
2008 *Ptychagnostus affinis* (Brøgger); Høyberget & Bruton, p. 50, pl. 7, figs N–X; pl. 8, figs A–D.
2009 *Ptychagnostus affinis* (Brøgger); Weidner & Nielsen, p. 260, figs 9A–C, 10C.
2010 *Ptychagnostus affinis* (Brøgger); Jago & Bentley, p. 475, fig. 6E–H.
2012 *Ptychagnostus affinis* (Brøgger); Buchholz, pl. 2, figs E–I.
2014 *Ptychagnostus affinis* (Brøgger); Weidner & Nielsen, p. 36 (*cum syn.*), fig. 13A–D.

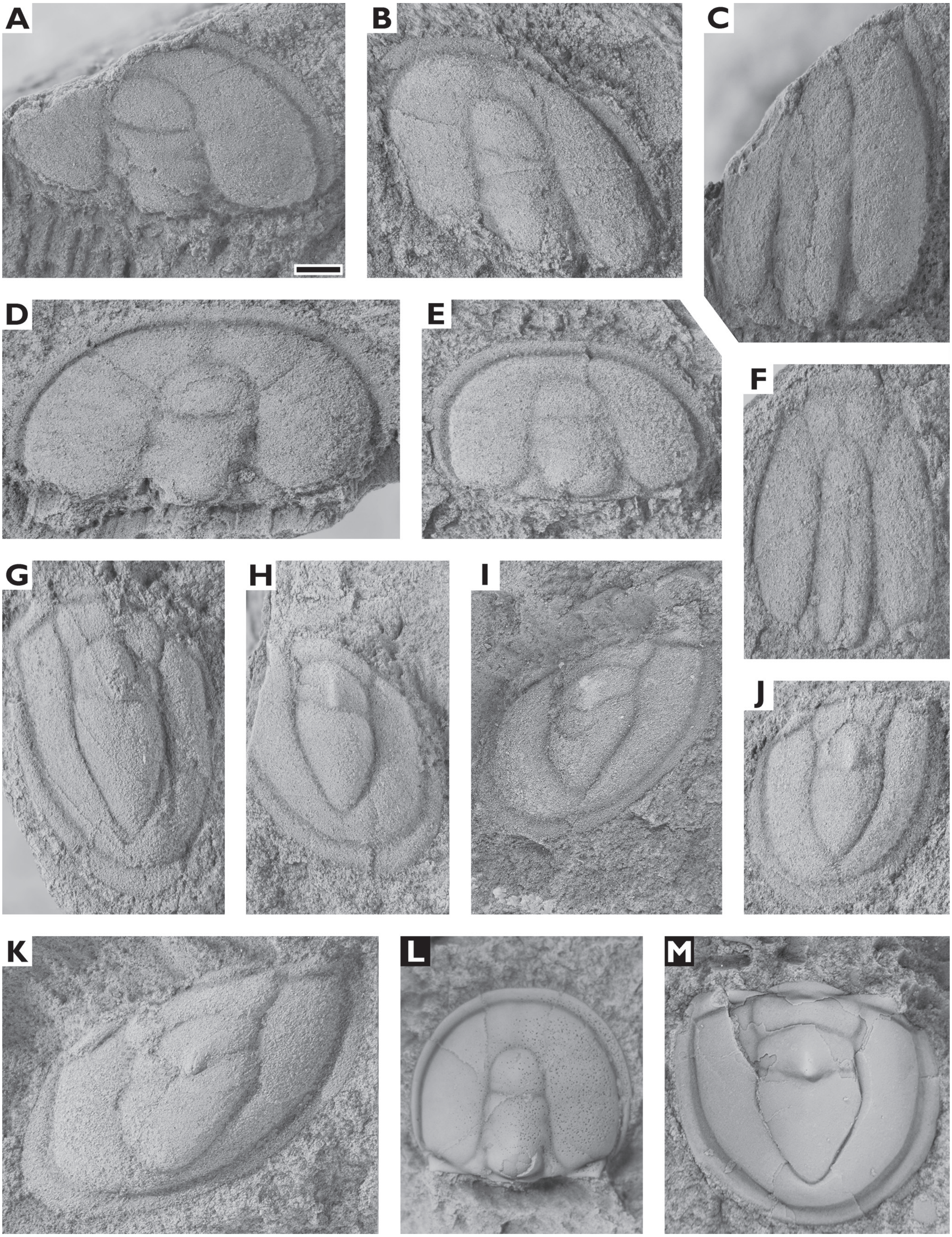


Fig. 22. ***Pentagnostus praecurrens*** (**Westergård, 1936**), *A. pinus – P. praecurrens* Zone. **A**–**F**, cephala. PMU 31623, 31622, 31621, 31618, 31628, 31620. **G**–**K**, pygidia. PMU 26139, 31638, 31630/1, 31629, 31631. A–K are from Hemfjäll. L, undeformed cephalon from Viken 2, Jämtland, PMU 25923, and M, undeformed pygidium from Klocksåsen, Jämtland, PMU 25908. Both are from autochthonous strata and have previously been illustrated by Weidner & Ebbestad (2014, fig. 4D and 6J). Scale bar = 1 mm.

Lectotype (designated by Høyberget & Bruton 2008). – Cephalon, PMO 28148, originally figured by Brøgger (1878, pl. 5, fig. 2a) and refigured by Høyberget & Bruton (2008, plate 7, fig. O). It derives from the upper part of the *A. atavus Zone* or the lower part of the *P. punctuosus* Zone in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Material and occurrence. – The species, in total represented by a little more than 30 specimens, has been found at Djupdalsbäcken, Strömnäs, Granberget, Fånån and Abborrfallet (northern Jämtland) and at Högnäsån, Karbäcken, Kvarnbäcken and Bellviks Hällan on the Tåsjö Mountain. All are from the *A. atavus* Zone. The species is known from various localities in Sweden, Norway and Bornholm (Brøgger 1878; Westergård 1946; Høyberget & Bruton 2008; Weidner & Nielsen 2009, 2014), where it has a range from the *A. atavus* Zone to the *P. punctuosus* Zone. Elsewhere it has been reported e.g. from the *A. atavus* Zone of Greenland (Robison 1994) and China (Peng & Robison 2000) and from the *P. punctuosus* Zone in USA (Robison 1984), Antarctica (Wolfart 1994) and Australia (Öpik 1979; Jago & Bentley 2010).

Remarks. – *Ptychagnostus affinis* resembles *A. atavus*. Differences in the cephalon of these species mainly concern the position of the glabellar node, which is placed more forwards in *P. affinis*; Weidner & Nielsen (2009, fig. 10) provided comparative

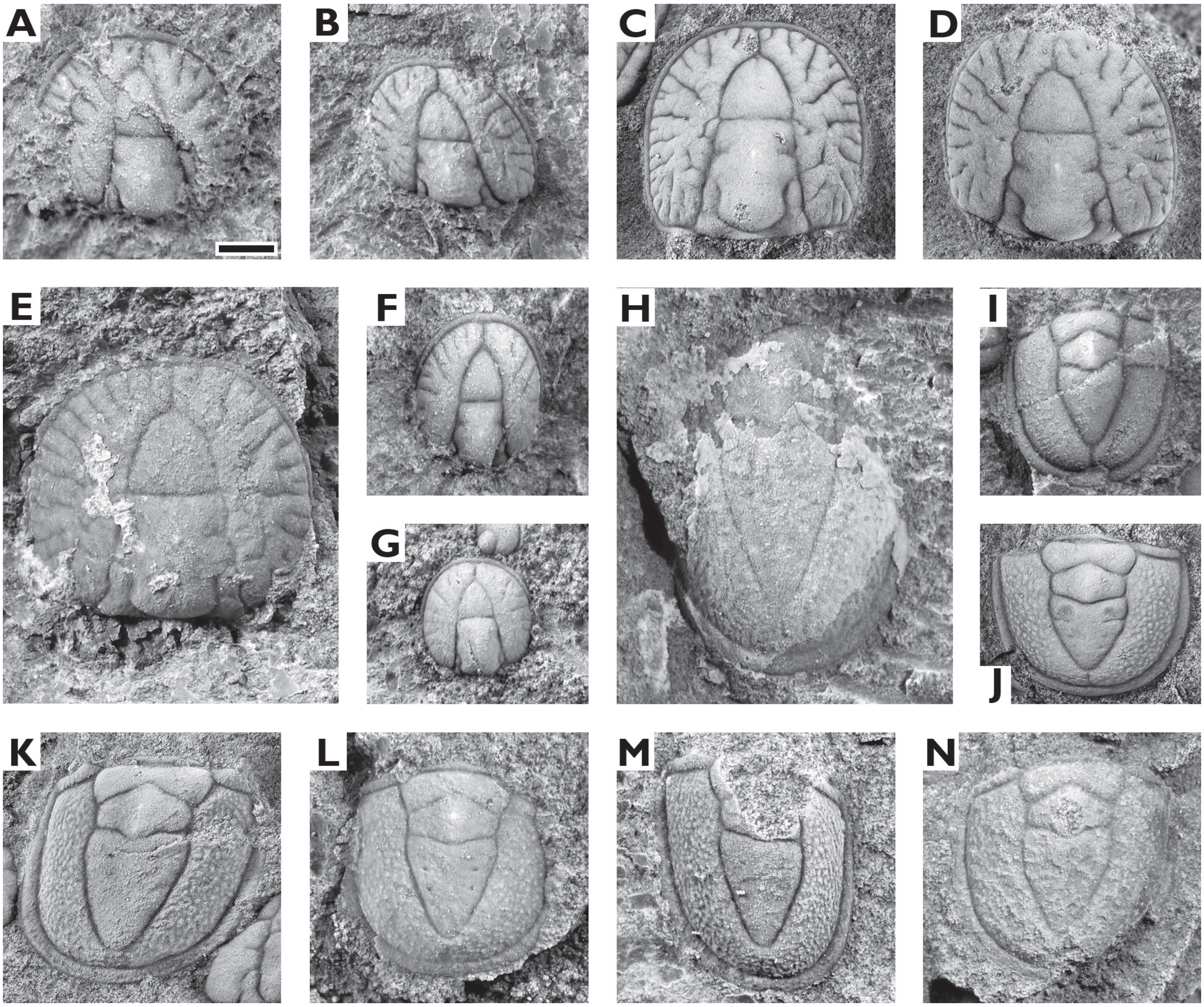


Fig. 23. ***Ptychagnostus affinis*** (**Brøgger, 1878**), *A. atavus* Zone. **A**–**G**, cephala. PMU 37136/1, 37133, 26216, 26214/1, 37135, 37136/2, 37131/6. **H**–**N**, pygidia. PMU 37132/3, 37137, 26214/2, 26217, 37132/2, 37138, 37139. A, F and I are from Djupdalsbäcken, A and F displaying the glabellar node in an intermediate position between *A. atavus* and *P. affinis*. B, E, H and L–N are from Strömnäs, C–D and J with an incipient F3 furrow and K are from Fånån, G is from Granberget. Scale bar = 1 mm.

illustrations. The posteroaxis in the pygidium of *P. affinis* is less convex than in *A. atavus* and shows a granulate surface and generally three or four pairs of impressions (Westergård 1946; Høyberget & Bruton 2008; Weidner & Nielsen 2009, 2014). Cephala and pygidia intermediate between *A. atavus* and *P. affinis* occur (Westergård 1946, pl. 11, figs 24, 25; Weidner & Nielsen 2009, fig. 10B and 2014, fig. 11G, H).

Our new cephala are identified as *affinis* by the glabellar node immediately in front of F2 whereas the pygidia are identified by the depressed posteroaxis with 3 to 4 paired impressions and the faint granulation of the pleural fields. One pygidium (Fig. 23J) shows an incipient F3 half-way across the axis instead of the first pair of impressions. None of the strongly furrowed cephala show arcuate furrows, as often seen in *A. atavus* (Fig. 16G, H).

Genus *Tomagnostus* Howell, 1935c

Type species (OD). – *Agnostus fissus* Lundgren *in* Linnarsson, 1879, from the Exsulans Limestone Bed, *T. gibbus* Zone, near Brantevik, Scania, Sweden.

Diagnosis. – See Robison (1994) and Shergold & Laurie (1997).

Remarks. – Five species are reported from the Miaolingian of Scandinavia, viz. *T. fissus* (Lundgren in Linnarsson, 1879), *T. perrugatus* (Grönwall, 1902), *T. sibiricus* Pokrovskaya & Egorova in Savitsky *et al.*, 1972, *T. bothrus* Robison, 1994, and *T. brantevikensis* Weidner & Nielsen, 2016.

Tomagnostus perrugatus **(Grönwall, 1902)**

Figure 24A, B

1902 *Agnostus fissus* Lundgren MS., var. *perrugata* n. var. Grönwall, p. 50, pl. 1, fig. 1.
1946 *Tomagnostus perrugatus* (Grönwall); Westergård, p. 59, pl. 8, figs 1–10.
1972 *Tomagnostus perrugatus* (Grönwall); Pokrovskaya & Egorova *in* Savitsky *et al.*, pl. 5, figs 7– 10.
1979 *Tomagnostus perrugatus* (Grönwall); Rushton, p. 55 (*cum syn.*), figs 6C–E.
2006c *Tomagnostus perrugatus* (Grönwall); Mischnik, p. 125, pl. 1, figs 12–15.
2014 *Tomagnostus perrugatus* (Grönwall); Weidner & Nielsen, p. 44, fig. 20A–F.
2015b *Tomagnostus perrugatus* (Grönwall); Weidner & Nielsen, fig. 11K–T.
2016 *Tomagnostus perrugatus* (Grönwall); Weidner & Nielsen, fig. 3 (*cum syn.*).

Holotype (by monotypy). – Cephalon, MGUH 143 (Grönwall 1902, pl. 1, fig. 1) from the upper part of the *A. atavus* Zone, Alum Shale Formation, at Øleå, Bornholm, Denmark. The specimen was refigured by Weidner & Nielsen (2014, fig. 20A).

Material and occurrence. – One cephalon was found in the *A. atavus* Zone at Högnäsån on the Tåsjö Mountain. In Scania, *T. perrugatus* occurs at Andrarum and Brantevik where it ranges from the *T. gibbus* Zone to the upper part of the *A. atavus* Zone. It is generally infrequent and rare in the upper part of the *A. atavus* Zone (Westergård 1946). Our own collections from Brantevik are all from the *T. gibbus* Zone (Weidner & Nielsen 2015b). The species is known also from Närke, but is rare (Westergård 1946). On Bornholm the species is rare and was collected from the lower and upper part of the *A. atavus* Zone (Weidner & Nielsen 2014). For worldwide distribution, see Weidner & Nielsen (2014).

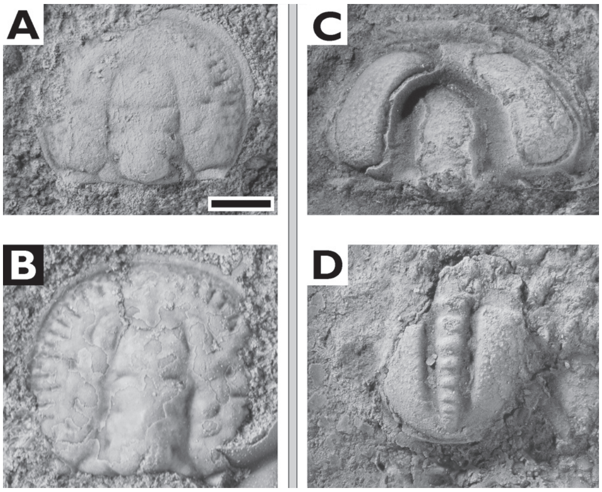


Fig. 24. ***Tomagnostus perrugatus*** (**Grönwall, 1902**), *A. atavus* Zone. PMU 26107, 27362. **A**, cephalon from Högnäsån, **B** is a better preserved cephalon from Brantevik, Scania, for comparison. The latter has previously been illustrated by Weidner & Nielsen (2015b, fig. 11L). ***Eodiscus punctatus*** (**Salter, 1864**), *P. punctuosus* Zone. **C**, cranidium. PMU 26222. **D**, pygidium. PMU 26221/1. Both are from Abborrfallet. Scale bar = 1 mm.

Remarks. – We assign the cephalon to *T. perrugatus* based on its overall shape, the narrow border and border furrow, the segmented posteroglabella with distinct glabellar furrows, the paired arcuate furrows and the straight radiating scrobicules all around the cheeks.

Tomagnostus perrugatus resembles *T. brantevikensis*, occurring in the same stratigraphical interval at Brantevik (Weidner & Nielsen 2016). *Tomagnostus brantevikensis* has a strongly tapering posteroglabella whereas it is typically parallel-sided in *T. perrugatus*; *T. brantevikensis* further shows a deltoid depression at the anterior midpoint. The pygidium of *T. brantevikensis* lacks short lateral spines that are present in *T. perrugatus* and the axial node is more elongate than in *T. perrugatus*, extending for the entire length of M2.

Representatives of *Tomagnostus* are extremely rare in the Caledonides. Apart from this one specimen of *T. perrugatus*, only one specimen of *T. fissus* has been found on the Norwegian side of the range (Høyberget & Bruton 2008).

Genus *Triplagnostus* Howell, 1935c

Type species (OD). – *Agnostus gibbus* Linnarsson, 1869, from the *T. gibbus* Zone, Alum Shale Formation, at Hunneberg, Västergötland, Sweden.

Diagnosis. – See Öpik (1979) and Shergold & Laurie (1997).

Remarks. – One species, *T. gibbus* (Linnarsson, 1869), is described from the Miaolingian of Scandinavia. Other authors assign *gibbus* to *Ptychagnostus* (Robison 1994; Axheimer & Ahlberg 2003; Fletcher 2006; Høyberget & Bruton 2008).

Triplagnostus gibbus (Linnarsson, 1869)

Figure 25A–T

1869 *Agnostus gibbus* n. sp. Linnarsson, p. 81, pl. 2, fig. 52.
1878 *Agnostus gibbus* Linnarsson; Brøgger, p. 62, pl. 6, fig. 11a, b.
1879 *Agnostus gibbus* Linnarsson; Linnarsson, p. 22, pl. 2, figs 31, 32.
1880 *Agnostus gibbus* Linnarsson; Tullberg, p 15, pl. 1, figs 2a–c.
1929 *Agnostus gibbus* Linnarsson; Strand, p. 343.
1935c *Triplagnostus gibbus* (Linnarsson); Howell, p. 14, pl. 1, figs 5, 6 [*Triplagnostus* erected].
1936 *Triplagnostus gibbus* Linnarsson; Whitehouse, p. 84, pl. 8, figs 6, 7; pl. 10, figs 1 (*pars*), 2.
1943 *Triplagnostus gibbus* (Linnarsson); Westergård, p. 44, fig. 15.
?1946 *Ptychagnostus* (*Triplagnostus*) *angermanensis* n. sp. Westergård, p. 70, pl. 9, figs 15, 16.
1946 *Ptychagnostus* (*Triplagnostus*) *gibbus* (Linnarsson); Westergård, p. 70, pl. 9, figs 17–24.
1964 *Ptychagnostus* (*Triplagnostus*) *gibbus* (Linnarsson); Orlowski, p. 66.
1967 *Ptychagnostus gibbus* (Linnarsson); Rasetti, p. 28, pl. 10, figs 1–8.
1969 *Triplagnostus gibbus* (Linnarsson); Egorova & Savitsky, p. 102, pl. 5, figs 10, 11.
1972 *Triplagnostus gibbus* (Linnarsson); Pokrovskaya & Egorova *in* Savitsky *et al.*, p. 60, pl. 5, figs 1–6.
1972a *Ptychagnostus* n. sp.? Robison, p. 245, fig. 3C.
1976 *Triplagnostus gibbus* (Linnarsson); Egorova *et al.*, p. 60, pl. 54, figs 9–15; pl. 55, figs 7, 8; pl. 58, fig. 10.
1976 *Triplagnostus pictinatus* Pokrovskaya & Egorova, sp. n. Egorova *et al.*, p. 63, pl. 36, figs 15, 16; pl. 38, figs 1–4, 23, 24; pl. 55, figs 1, 2; pl. 59, fig. 4.
1979 *Triplagnostus gibbus gibbus* (Linnarsson); Öpik, p. 117, pl. 23, figs 1–3; textfig. 36.
1979 *Triplagnostus gibbus posterus* subsp. nov. Öpik, p. 119, pl. 23, figs 4, 5; pl. 24, figs 1–5; pl. 25, figs 1–3; pl. 27, fig. 2.
1979 *Triplagnostus quasigibbus* sp. nov. Öpik, p. 120, pl. 27, fig. 1.
1979 *Triplagnostus fretus* sp. nov. Öpik, p. 121, pl. 28, figs 1–6.
1979 *Triplagnostus diremptus* sp. nov. Öpik, p. 122, pl. 22, fig. 1; pl. 26, figs 1, 2, 4–6.
1980 *Triplagnostus gibbus* (Linnarsson); Ergaliev, p. 72, pl. 1, figs 11, 12.
1982 *Ptychagnostus* cf. *P. gibbus* (Linnarsson); Kindle, pl. 1.1, figs 13, 18.
1982 *Triplagnostus gibbus* (Linnarsson); Egorova *et al.*, p. 64, pl. 1, fig. 1; pl. 2, fig. 2; pl. 3, fig. 4a; pl. 52, figs 3, ?4.
1982 *Ptychagnostus gibbus* (Linnarsson); Robison, p. 139, pl. 2, figs 1–13.
1982 *Ptychagnostus gibbus*; Rowell, Robison & Strickland, p. 161.
1984 *Ptychagnostus gibbus* (Linnarsson); Robison, p. 22, fig. 13.
1988 *Triplagnostus* (*Triplagnostus*) *gibbus* (Linnarsson); Laurie, p. 196, fig. 16A–O.
1989 *Ptychagnostus gibbus* (Linnarsson); Young & Ludvigsen, p. 12, pl. 2, figs 13–16.
1990 *Triplagnostus* (*Triplagnostus*) *gibbus* (Linnarsson); Shergold, Laurie & Sun, p. 78, fig. 12:5a, b.
1994 *Ptychagnostus gibbus* (Linnarsson); Robison, p. 56, fig. 27:3, 4.
pars 1994 *Triplagnostus gibbus* (Linnarsson); Rudolph, p. 129, pl. 6, figs 2–7, *non* fig. 1 [= *Tomagnostus sibiricus* Pokrovskaya & Egorova *in* Savitsky *et al.*, 1972].
1997 *Triplagnostus* (*Triplagnostus*) *gibbus* (Linnarsson); Shergold & Laurie, fig. 225:1a, b.
1999 *Triplagnostus gibbus* (Linnarsson); Fedoseev, pl. 2, figs 2, 4.
2000 *Triplagnostus gibbus* (Linnarsson); Pegel, fig. 10:16.
2000 *Ptychagnostus gibbus* (Linnarsson); Peng & Robison, 71, fig. 54.
2003 *Ptychagnostus gibbus* (Linnarsson); Axheimer & Ahlberg, p. 147, fig. 5D–G.
2006 *Ptychagnostus gibbus* (Linnarsson); Fletcher, pp. 86, 117.
2006c *Ptychagnostus gibbus* (Linnarsson); Mischnik, p. 132, pl. 1, figs 6–9.
2008 *Triplagnostus gibbus* (Linnarsson); Ergaliev & Ergaliev, p. 127, pl. 2, figs 18–20.
2008 *Ptychagnostus gibbus* (Linnarsson); Høyberget & Bruton, p. 51, pl. 8, figs N–S.
2009 *Triplagnostus gibbus* (Linnarsson); Weidner & Nielsen, p. 263, fig. 13A–D.
2012 *Triplagnostus gibbus* (Linnarsson); Buchholz, pl. 1, figs M–O; pl. 2, fig. A.
2015b *Triplagnostus gibbus* (Linnarsson); Weidner & Nielsen, fig. 5E–H.
2016 *Triplagnostus gibbus* (Linnarsson); Pegel, Egorova, Salikhova & Shabanov, pl. 9, figs 1, 2.
2016 *Triplagnostus gibbus* (Linnarsson); Korovnikov & Shabanov, pl. 2, fig. 18.

Lectotype. – Designated here, pygidium SGUR 11020/02, one of Linnarsson's syntypes from the *T. gibbus* Zone at Vittene, Hunneberg, Västergötland, Sweden. It is here illustrated in Figure 25A.

Paralectotype. – Cephalon SGUR 11020/04, from the same bedding plane as the lectotype (Fig. 25B).

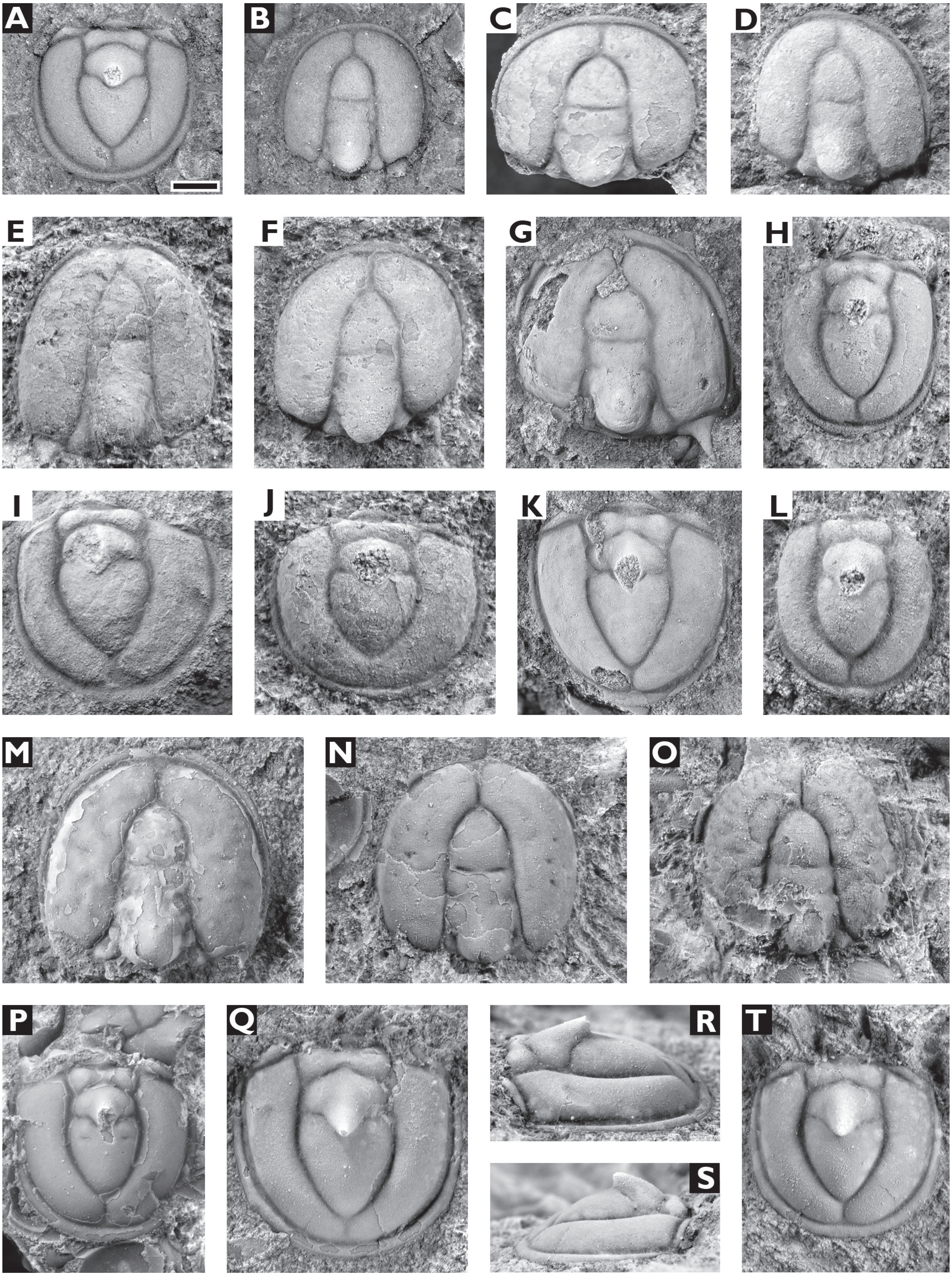


Fig. 25. ***Triplagnostus gibbus*** **(Linnarsson, 1869)**, *T. gibbus* Zone. **A, lectotype** pygdium and **B**, paralectotype cephalon from Vittene, Hunneberg, Västergötland. SGUR 11020/04 and SGUR 11020/02. **C**–**F**, cephala from Strömnäs. PMU 36425, 37142, 36422, 36424. **G**, cephalon from Sågbäcken with posterior cephalic spine. PMU 26110. **H**–**J** and **L**, pygidia from Strömnäs. PMU 37145, 37140, 36423, 37144. **K**, pygidium from Sågbäcken. PMU 26109. **M**–**T**, cephala and pygidia from ice-rafted boulders, As Hoved, Denmark, to supplement the taxonomic description. MGUH 34037–34042. M with slight scrobiculated surface, N with pitted surface, O with stronger scrobiculation and a distinct pair of arcuate furrows. P showing the typical view of a pygidium with the node broken off. Note also the shallow F3 furrows. Q–R and S–T show two pygidia in dorsal and lateral views with intact axial nodes. Scale bar = 1 mm.

Material and occurrence. – About 30 cephala and pygidia of *T. gibbus*, many ill-preserved, were collected at Strömnäs. Kulling (1955) recorded the species also from Långseleån, Granhöjden near Strömnäs, Skikkisjö Mountain and Lubbträsk. At Abborrfallet and at Sågbäcken on the Tåsjö Mountain, *T. gibbus* occurs, but is rare. The species occurs alone or in few cases associated with *A. acadicus*. Elsewhere in Scandinavia, *T. gibbus* is recorded from many provinces of Sweden (Westergård 1946) and Norway (Høyberget & Bruton 2008). It also occurs in ice-rafted boulders at As Hoved, Denmark, with provenance from Västergötland (Fig. 25M–T) and in northern Germany (Rudolph 1994; Mischnik 2006c). Outside Scandinavia, it is reported from Poland (Orlowski 1964), Siberia (Egorova *et al.* 1982; Pegel 2000), Kazakhstan (Ergaliev 1980; Ergaliev & Ergaliev 2008), China (Peng & Robison 2000), USA (Rasetti 1967; Robison 1982), Laurentian Newfoundland, Canada (Young & Ludvigsen 1989), Greenland (Robison 1984), Australia (Öpik 1979; Laurie 1988) and Antarctica (Soloviev & Grikurov 1978). It generally occurs in the eponymous zone, but in Norway, Siberia, China and Australia it ranges into the *A. atavus* Zone. *Triplagnostus gibbus* is also listed by Fletcher (2006, not figured) from Avalonian Newfoundland. Previous records from that region published by Matthew (1896) have not been considered to represent *T. gibbus* (Öpik 1979; Robison 1982; Høyberget & Bruton 2008). Another report of this species from England (Cobbold & Pocock 1934) is regarded as very uncertain (Robison 1982, based on a written evaluation from Rushton).

Remarks. – Australian specimens of *Triplagnostus* were treated by Öpik (1979). Based on a number of cephalic and pygidial criteria, mainly the presence or absence of lateral pygidial spines, the shape of the basal lobes and the length of the cephalic spines and axial spines on the posterior segment of the thorax, he distinguished *T. gibbus posterus* and a couple of closely similar species. Robison (1982) considered the distinguishing features to be intraspecific variation and most of the Australian species coexisting with *T. gibbus* were treated as junior synonyms by Robison (1982) and Laurie (1988).

Our new material complies fully with illustrations of *T. gibbus* from Sweden (Westergård 1946; Weidner & Nielsen 2009), ice-rafted boulders with origin from Sweden (Rudolph 1994; Mischnik 2006c) and Norway (Høyberget & Bruton 2008). Characteristic for this species is the rounded base of a broken off axial node in the pygidium (Tullberg 1880, pl. 1, fig. 2b; Westergård 1946, pl. 9, figs 18, 24; Høyberget & Bruton 2008, pl. 8, figs N–Q) and the lack of lateral spines. The cephalon has elongated basal lobes and posterior spines of variable length.

Discussion. – None of the pygidia hitherto illustrated from Scandinavia allow assessment of whether M2 carries a node or a spine, as only the base of a broken off extension is visible. Tullberg (1880), Westergård (1946), Mischnik (2006c), Høyberget & Bruton (2008) and Weidner & Nielsen (2009) described it as a spine, whereas Rudolph (1994) considered it as a node. Material of *T. gibbus* collected from ice-rafted boulders at As Hoved, Denmark, with origin from Västergötland, includes few pygidia that have the M2 extension preserved and we agree with Rudolph that the term node is preferable (Fig. 25Q–T). In pygidia from Australia (Laurie 1988), China (Peng & Robison 2000) and USA (Robison 1982), the axial extension, however, is developed as a spine. Within the same ice-rafted material from Västergötland, some cephala have a pitted surface of the cheeks and arcuate furrows and the pygidia often carry a secondary, tiny node on the posteroaxis (Fig. 25M–T). One pygidium shows short, shallow abaxial furrows at the F3 position (Fig. 25P) (see also Fig. 23J, for *P. affinis* and Weidner & Nielsen 2014, fig. 11E, for *A. atavus*).

Family Spinagnostidae Howell, 1935a

Genus *Cotalagnostus* Whitehouse, 1936

Type species (OD). – *Agnostus lens* Grönwall, 1902, from the *P. punctuosus* Zone, Alum Shale Formation at Øleå, Bornholm, Denmark.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – For brief discussion of genus, see Westergård (1946) and Peng & Robison (2000, p. 60).

Four species, *C. lens* (Grönwall, 1902), *C. confusus* (Westergård *in* Holm & Westergård, 1930), *C. claudicans* Westergård, 1946 and *C. greilingi* n. sp., are known from the Miaolingian of Scandinavia.

Cotalagnostus claudicans Westergård, 1946

Figure 27S–T

1946 *Cotalagnostus lens claudicans* subsp. n. Westergård, p. 54, pl. 6, figs 20–27.
1962 *Cotalagnostus lens* (Grönwall) subsp. *C. claudicans* Westergård; Hutchinson, p. 76, pl. 6, figs 18–20.
1982 *Cotalagnostus lens claudicans* Westergård; Egorova *et al.*, p. 72, pl. 56, figs 1–3, 5.
?1991 *Cotalagnostus lens claudicans* Westergård; Yang *et al.*, p. 114, pl. 5, figs 14, 15.

pars 2008 *Cotalagnostus lens* (Grönwall); Høyberget & Bruton, p. 42, pl. 6, fig. E.
2014 *Cotalagnostus claudicans* Westergård; Weidner & Nielsen, p. 51 (*cum syn.*), fig. 24A–D.

Holotype. – Cephalon, SGU 4814, figured by Westergård (1946, pl. 6, fig. 20); collected from a boulder at Gislövshammar, Scania, Sweden, representing the lower part of the *A. atavus* Zone in the Alum Shale Formation.

Material and occurrence. – One cephalon from the *A. atavus* Zone at Granberget. In Scandinavia, *C. claudicans* has a range from the lower part of *A. atavus* Zone into the *P. punctuosus* Zone; for details, including occurrences outside Scandinavia, see Weidner & Nielsen (2014).

Remarks. – For remarks on *C. claudicans* and comparison with *C. lens* (Grönwall, 1902), see Weidner & Nielsen (2014). We assign our cephalon to *C. claudicans* as the glabellar node is situated behind midpoint of the cephalon. In *C. lens* the node is placed centrally.

Cotalagnostus confusus (Westergård *in* Holm & Westergård, 1930)

Figure 26A–H

1878 *Agnostus bituberculatus*, Angelin; Brøgger, p. 75, pl. 6, fig. 9.
1930 *Agnostus confusus* n. sp. Westergård *in* Holm & Westergård, p. 12, pl. 4, figs 7, 8.
1946 *Cotalagnostus confusus* (Westergård); Westergård, p. 54, pl. 7, figs 6–20.
?1991 *Cotalagnostus confusus* (Westergård); Yang *et al.*, p. 114, pl. 5, fig. 13.
2008 *Cotalagnostus confusus* (Westergård *in* Holm & Westergård); Høyberget & Bruton, p. 43, pl. 6, figs G–N.

Lectotype. – Designated here, pygidium SGU 5460, one of Westergård's syntypes from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden (Fig. 26H). The specimen was illustrated previously by Westergård *in* Holm & Westergård (1930, pl. 4, fig. 8) and Westergård (1946, pl. 7, fig. 13).

Paralectotype. – Cephalon SGU 5459, from the same locality (Fig. 26G). The specimen was illustrated previously by Westergård in Holm & Westergård (1930, pl. 4, fig. 7) and Westergård (1946, pl. 7, fig. 6).

Material and occurrence. – Three cephala and three pygidia were collected from the lower part of the *L. laevigata* Zone at Långseleån and Fjällbränna, all poorly preserved and deformed. Another pygidium is from Högnäsån on the Tåsjö Mountain. Elsewhere in Sweden, *C. confusus* occurs infrequently in the lower part of the *L. laevigata* Zone in Scania, Västergötland and Närke (Westergård 1946). The species is infrequent in ice-rafted boulders of the Exporrecta Conglomerate Bed at As Hoved, Denmark, with

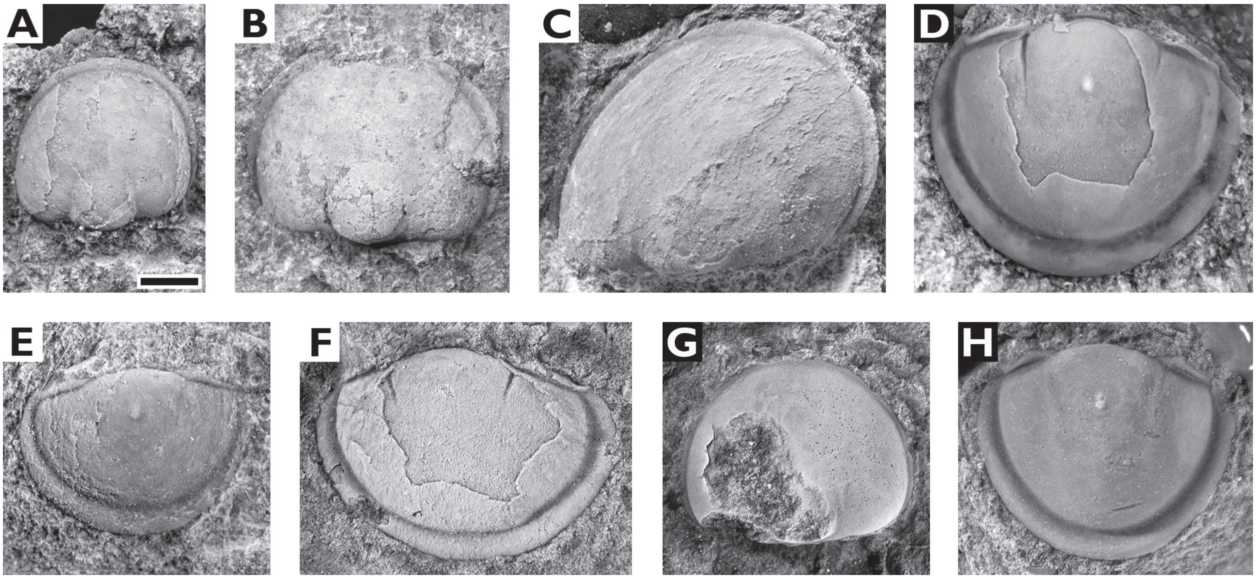


Fig. 26. **Cotalagnostus confusus (Westergård in Holm & Westergård, 1930)**, lower part of the *L. laevigata* Zone. **A**–**B** are cephala from Långseleån, **C** is from Fjällbränna. PMU 37147/1, 37148, 37149. **D** is a well-preserved pygidium from ice-rafted boulder, As Hoved, Denmark, to show proper pygidial proportions. MGUH 34043. **E** is a pygidium from Långseleån and **F** is from Högnäsån. PMU 37150, 26245/2. **G** shows the paralectotype cephalon, SGU 5459, previously illustrated by Westergård in Holm & Westergård (1930, pl. 4, fig. 7) and Westergård (1946, pl. 7, fig. 6). **H**, **lectotype** pygidium, SGU 5460, previously illustrated by Westergård in Holm & Westergård (1930, pl. 4, fig. 8) and Westergård (1946, pl. 7, fig. 13). G and H are from Andrarum, Scania. Scale bar = 1 mm.

provenance from Västergötland (collection TW). In Norway it is common in the same zone (Høyberget & Bruton 2008). *Cotalagnostus confusus* is confined to Scandinavia.

Remarks. – *Cotalagnostus confusus* is well-described by Westergård (1946) and Høyberget & Bruton (2008). The cephalon can be distinguished from similarly effaced species like *H. brevifrons*, *C. claudicans*, and *C. lens* by being wider than long. The pygidium is readily identified by being wider than long, the border is wide and widens rearwards, the strongly tapering axis fades out before reaching the half-length of the pygidium, and carries a prominent rounded node. Our new material (Fig. 26A–C, E, F) has a weathered surface and is partially tectonically deformed. Identification is based on agreement of the overall shape of the acrolobes and the borders and the rapidly tapering and fading out pygidial axis.

***Cotalagnostus greilingi* n. sp.**

Figure 27A–P

Derivation of name. – Named for Reinhard Greiling, Karlsruhe, Germany, for his major contribution to understanding the geology of the Scandinavian Caledonides.

Holotype (OD). – Pygidium, PMU 36420, Fig. 27I–K, from the lower part of the *L. laevigata* Zone in the Alum Shale Formation at Skansholm near Vilhelmina, Västerbotten.

Paratypes and occurrence. – Three cephala (PMU 36412/2, 36415, 35416/1) and 6 pygidia (36413, 35416/2, 36417–36419, 36421) were collected at the type locality, associated with *H. pater*.

Diagnosis. – A *Cotalagnostus* species with the glabellar node placed behind cephalic midpoint and posterior axial furrows in the cephalon weakly outlined or effaced; a pygidium with weak axial furrows and a faint indication of a postaxial furrow. Both shields with narrow border and border furrow.

Description. – The cephalon is as wide as long, rounded in outline, moderately convex, and it has a tiny glabellar node located behind the cephalic midpoint. The border is narrow, tapering rearwards. The border furrow is narrow; the anterior axial and transglabellar furrows are effaced; the posterior axial furrows are weakly outlined or effaced. Basal lobes are simple, small and connected by a narrow occipital band. The pygidium is slightly wider than long, rounded in outline, highly convex and conical in posterior view. The border is narrow and slightly wider than in the cephalon; the border furrow is narrow. The axial furrows are weakly impressed and become fainter towards the rear. The axis occupies about 40% of the width of the pygidium, is widest at M1, and shows faint constrictions at F1 and F2. A distinct elongate node is located on M2. The pleural fields narrow posteriorly but are separated by an almost indiscernible postaxial furrow. On internal moulds the axial furrows in the cephalon and the pygidium as well as the postaxial furrow are readily recognizable (Fig. 27I, J, M). A tiny secondary node is placed close to the tip of the axis.

Remarks. – *Cotalagnostus greilingi* n. sp. differs only in the faint axial and postaxial furrows of the pygidium from *C. claudicans* (Fig. 27I versus 27T), which occurs in the *A. atavus* and *P. punctuosus* zones. Both share the glabellar node situated behind cephalic midpoint. *Cotalagnostus lens* from the *A. atavus* and *P. punctuosus* zones has distinct posterior cephalic axial furrows and the glabellar node is placed centrally or nearly so (Fig. 27A, D–E versus 27Q). Pygidia differ from those of *C. greilingi* n. sp. by having distinct axial furrows and lacking a postaxial furrow (Fig. 27F–P versus 27R). All three species bear a tiny secondary node at about 85% of the length of the pygidial axis from the anterior. It can be seen in Fig. 28F, I, J, L, M, R and T.

The differences from *C. confusus* (Fig. 26) from the lower part of the *L. laevigata* Zone are more pronounced; see Westergård (1946). The cephalon of *C. confusus* is wider than long, has short and distinct posterior axial furrows and the glabellar node is placed in the rear quarter of the cephalic length. In *C. greilingi* n. sp., the cephalon is as wide as long, the posterior axial furrows are weak and the glabellar node is placed slightly behind the cephalic midpoint. In pygidia of *C. confusus* the posterior part of the axial furrows are effaced, the border is wide and the axial node is rounded. In pygidia of *C. greilingi* n. sp., the axial furrows are posteriorly weakly impressed to nearly effaced, the border is narrow and the axial node is elongate.

The cephalon of *Cotalagnostus* sp. nov. *sensu* Fletcher & Greene (2013) from the *P. punctuosus* Zone of St. John`s Islands, southeastern Newfoundland, is identical in all features with *C. claudicans* and *C. greilingi* n. sp., including having the glabellar node placed behind midpoint. Fletcher & Greene (2013)

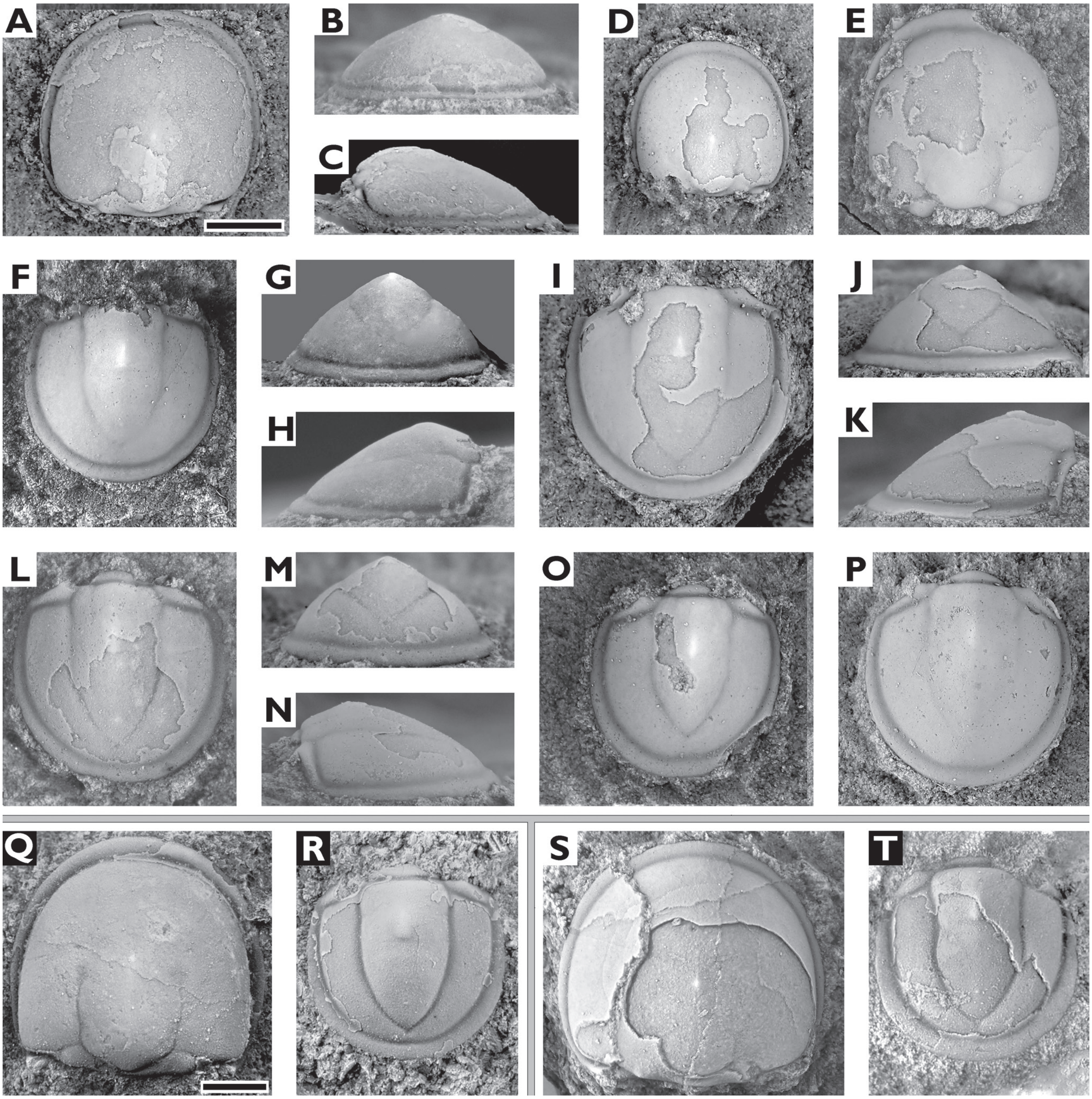


Fig. 27. ***Cotalagnostus greilingi* n. sp.** from the lower part of the *L. laevigata* Zone at Skansholm. **A**–**C**, cephalon in dorsal, anterior and lateral views. Glabellar node behind midpoint. PMU 36412/2. **D**–**E**, cephala. Glabellar nodes behind midpoint. PMU 36415 and PMU 36416. **F**–**H**, pygidium in dorsal, posterior and lateral views. Postaxial furrow very faint. PMU 36413. **I–K, holotype** pygidium in dorsal, posterior and lateral views. Note the secondary node. Postaxial furrow faint. PMU 36420. **L**–**N**, pygidium in dorsal, posterior and lateral views. PMU 36417. **O**–**P**, pygidia. PMU 36419 and PMU 36421/1. ***Cotalagnostus lens* (Grönwall, 1902)** for comparison. **Q**, **lectotype** cephalon from the *P. punctuosus* Zone, Øleå, Bornholm, Denmark. Glabellar node centrally. MGUH 149. It was previously illustrated by Grönwall (1902, pl. 1, fig. 8) and Weidner & Nielsen (2014, fig. 25A). **R**, pygidium from the *P. punctuosus* Zone, Øleå, Bornholm, Denmark. MGUH 30081. Note the secondary node. It was previously illustrated by Weidner & Nielsen (2014, fig. 25H–J). ***Cotalagnostus claudicans* Westergård, 1946**. **S**, cephalon from the *A.atavus* zone at Granberget. Glabellar node behind midpoint. PMU 36410. **T**, pygidium with distinct postaxial furrow, for comparison. Note the secondary node. Upper part of the *A. atavus* Zone, Øleå, Bornholm. Denmark. MGUH 30075. It was previously illustrated by Weidner & Nielsen (2014, fig. 24C). Scale bars = 1 mm. Scale bar in A is the same for A–P, scale bar in Q is the same for Q–T. Note that the magnification is larger than used for most agnostoid illustrations in this publication.

state that a glabellar node is absent, but in the illustrated material (*ibid*. pl. 1, figs 4, 5), a node is clearly recognizable. The pygidia, however, differ. The specimens from Newfoundland have a proportionally wider axis, occupying slightly more than half of the pygidial width, the axis is widest at the posteroaxis and terminates rounded. The axial furrows fade in the posterior half and a postaxial furrow is not present. The axis in the pygidium of *C. greilingi* n. sp. occupies about 40% of the pygidial width, is widest at M1, and terminates in a point. The axial furrows are less distinct than in the material from Newfoundland and they are separated beyond the tip of the axis by a postaxialfurrow. The material of *Cotalagnostus* sp. nov. from Newfoundland differs from *C. claudicans*, *C. greilingi* n. sp. and *C. lens* and represents another species, as yet unnamed.

Genus *Hypagnostus* Jaekel, 1909

Type species (OD). – *Agnostus parvifrons* Linnarsson, 1869, from the *Hypagnostus parvifrons* Zone, Alum Shale Formation at Kinnekulle, Västergötland, Sweden.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – For a brief discussion of genus, see Westergård (1946) and Peng & Robison (2000).

Eight species of *Hypagnostus* have been recorded in the Miaolingian of Scandinavia, viz. *H. brevifrons* (Angelin, 1851), *H. parvifrons* (Linnarsson, 1869), *H. mammillatus* (Brøgger, 1878), *H. truncatus* (Brøgger, 1878), *H. frontosa* (Grönwall, 1902), *H. lingula* (Grönwall, 1902), *H. clipeus* Whitehouse, 1939 and *H. tjernviki* Westergård, 1946.

***Hypagnostus brevifrons* (Angelin, 1851)**

Figure 28A–I

1851 *Agnostus brevifrons* n. sp. Angelin, p. 6, pl. 6, fig. 4.
1878 *Agnostus brevifrons*, Angelin; Brøgger, p. 73, pl. 6, fig. 10.
1878 *Agnostus laevigatus*, Dalman var. *similis* Brøgger, p. 74, pl. 6, fig. 6.
1880 *Agnostus brevifrons* Angelin; Tullberg, p. 35, pl. 2, fig. 29.
1902 *Agnostus brevifrons* Angelin; Grönwall, p. 76.
1946 *Hypagnostus brevifrons* (Angelin); Westergård, p. 48, pl. 5, figs 24–29.
1961 *Hypagnostus brevifrons* (Angelin); Öpik, p. 58, pl. 18, figs 6–10.
1963 *Hypagnostus brevifrons* (Angelin); Lu, p. 27, pl. 2, figs 12–15.
1965 *Hypagnostus brevifrons* (Angelin); Lu, Zhang, Zhu, Qian & Xiang, p. 44, pl. 4, figs 21–24.
non 1970 *Hypagnostus brevifrons* (Angelin); Hajrullina, p. 13, pl. 1, fig. 2 [= indet.].
pars 1973 *Hypagnostus brevifrons* (Angelin); Hajrullina, p. 42, pl. 2, figs 6, 9?, 11, *non* fig. 12 [= indet.].
non 1975 *Hypagnostus brevifrons* (Angelin); Repina, Petrunina & Hajrullina, p. 116, pl. 10, figs 7–10 [7 = *Tomagnostella exsculpta*; 8–10 = *Hypagnostus parvifrons*]; pl. 11, figs 1–3 [1 = *Tomagnostella exsculpta*; 2, 3 = indet.].
1976 *Hypagnostus* cf. *brevifrons* (Angelin); Jago, p. 5, pl. 1, figs 1–4.
1977 *Hypagnostus brevifrons* (Angelin); Fedjanina, p. 147, pl. 19, figs 7, 8, 10, 11, 13.
1980 *Hypagnostus brevifrons* (Angelin); Ergaliev, pl. 4, figs 9–11.
1981 *Hypagnostus brevifrons* (Angelin); Zhang, p. 143, pl. 55, figs 15–17; pl. 56, fig. 7.
pars 1982 *Hypagnostus brevifrons* (Angelin); Egorova *et al*., p. 70, pl. 18, fig. 5; pl. 21, fig. 3; pl. 34, fig. 17; *non* pl. 21, fig. 5 & pl. 46, fig. 2a [= indet.].
1982 *Hypagnostus brevifrons* (Angelin); Yang, pl. 2, figs 6, 7.
1985 *Hypagnostus brevifrons* (Angelin); Xiang & Zhang, p. 67, pl. 17, figs 11, 12.
1991 *Hypagnostus brevifrons* (Angelin); Yang *et al*., p. 111, pl. 4, figs 7, 8.
1994 *Hypagnostus brevifrons* (Angelin); Rudolph, p. 133, pl. 7, figs 1–3.
2000 *Hypagnostus brevifrons* (Angelin); Peng & Robison, p. 63 (*cum syn*.), fig. 46.
2001 *Hypagnostus brevifrons* (Angelin); Jago & Brown, p. 8, pl. 2, fig. H.
2002 *Hypagnostus brevifrons* (Angelin); Schöning, fig. 13.
2008 *Hypagnostus brevifrons* (Angelin); Høyberget & Bruton, p. 40, pl. 4, figs U–X.
2008 *Hypagnostus brevifrons* (Angelin); Ergaliev & Ergaliev, p. 130, pl. 9, figs 10–13; pl. 15, figs 1–13; pl. 19, fig. 8; pl. 24, figs 7–10, 14.
pars 2009b *Hypagnostus brevifrons* (Angelin); Peng *et al*., p. 22, figs 9:18b; 12:13–12:14 & 12:16–12:22; 15:10; *non* 12:15 [*Acadagnostus scutalis*?].
2014 *Hypagnostus brevifrons* (Angelin); Bentley & Jago, p. 271, fig. 3G–I.

Lectotype (designated by Westergård 1946). – Cephalon, NRM Ar9514, illustrated by Westergård (1946, pl. 5, fig. 24). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, Andrarum, Scania.

Material and occurrence. – Only one pygidium was found at Fjällbränna. Limestones from the lower part of the *L. laevigata* Zone are rare in the Vilhelmina area, but the species is quite common at various localities in the Allochthon on the Tåsjö Mountain (Högnäsån) and northern Jämtland (Vedjeön, Abborrfallet, Siljeåsen). Other reports are from Karbäcken (Asklund & Thorslund 1935) and Marbäcken (Kulling 1955). *Hypagnostus brevifrons* is recorded from many Swedish provinces (Westergård 1946), Norway (Høyberget & Bruton 2008), and Bornholm, Denmark (Grönwall 1902), but is generally infrequent. It is also described from ice-rafted boulders found in northern Germany (Rudolph 1994; Schöning 2002). Outside Scandinavia, the species is

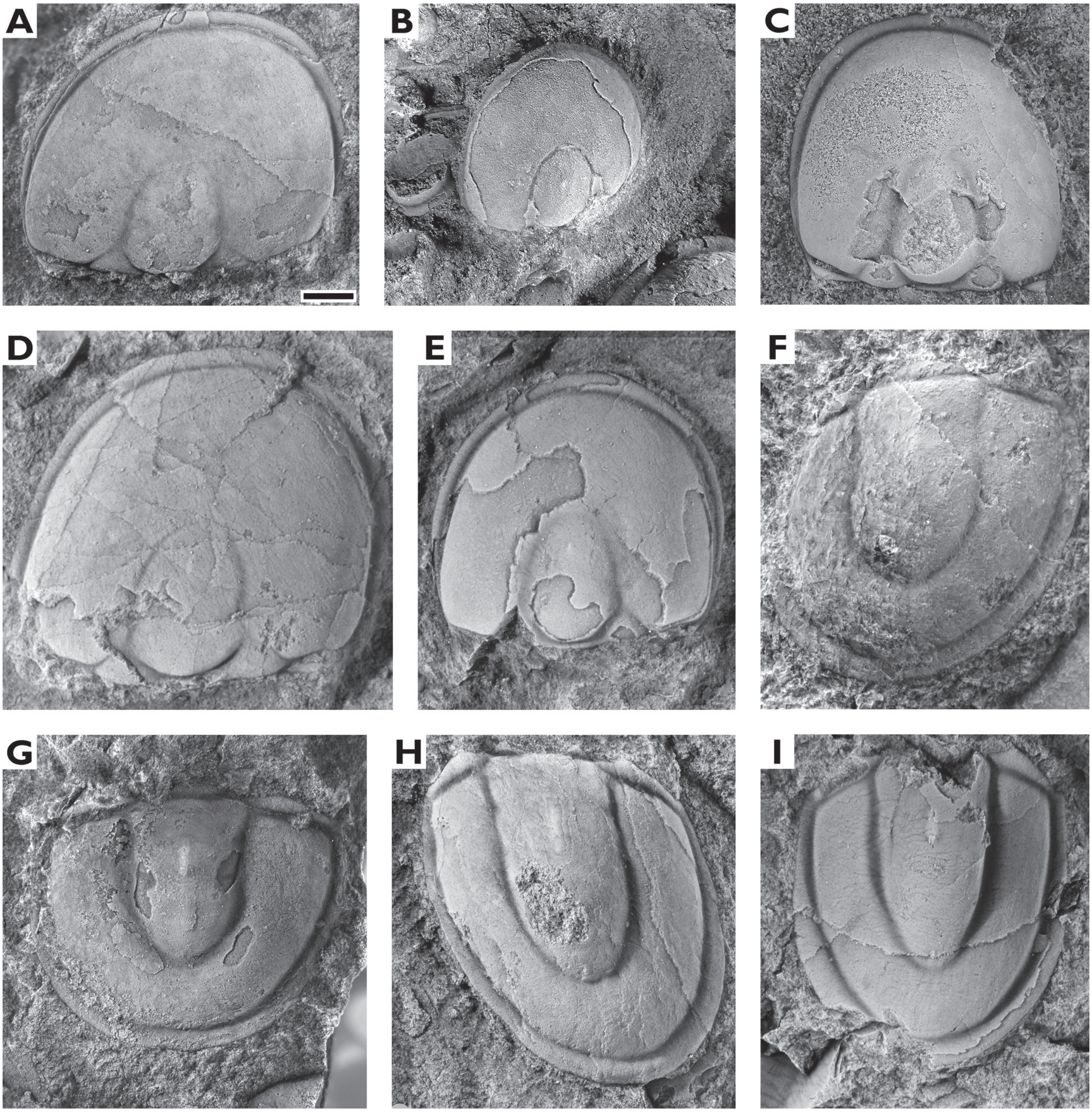


Fig. 28. ***Hypagnostus brevifrons*** **(Angelin, 1851)**, from the lower part of the *L. laevigata* Zone. **A–E**, cephala. PMU 26186, 26245/1, SGU 9893, 9895, 9900. **F–I**, pygidia. PMU 37152, 26155, 26605/1, SGU 9899. A, C and G are from Vedjeön, B is from Högnäsån, D–E, H and I are from Abborrfallet, F is from Fjällbränna. Scale bar = 1 mm.

reported from Siberia (Egorova *et al*. 1982) and the Salair, Russia (Fedjanina 1977), Kazakhstan (Ergaliev & Ergaliev 2008), the Turkestan range (Hajrullina 1970, 1973), Indian Himalaya (Peng *et al*. 2009b) and Australia (Öpik 1961; Jago & Brown 2001; Bentley & Jago 2014). It occurs everywhere in strata equivalent to the lower part of the *L. laevigata* Zone, except in China, where it has a long range from the *P. punctuosus* Zone into the basal Furongian (Peng & Robison 2000).

Remarks. – In material from Scandinavia, the characteristic trait of the cephalon is the rapidly tapering glabella, ovate in outline, occupying less than half of the cephalic length (see Angelin 1851, pl. 6, fig. 4; Westergård 1946, pl. 5, figs 24, 25, 28; Rudolph 1994, pl. 7, figs 1, 2; Høyberget & Bruton 2008, pl. 4, figs U, W). In comparison, *H. parvifrons* has a rounded (Fig. 31A, C) or truncate glabella with rounded anterior corners (Fig. 31B, Q) whereas *H. frontosa* (Weidner & Nielsen 2014, fig. 22A–H), *H. truncatus*

(Fig. 32), *H. lingula* (Fig. 29) and *T. exsculpta* (Fig. 33) all have a parallel-sided glabella ending truncately or slightly angulate. *Hypagnostus brevifrons* also has a weak node on the anterior half of the glabella, a narrow border and border furrow. The pygidium has wide confluent pleural fields of approximately even width and an unsegmented axis which may vary in length and width and has a gently rounded termination. The axis carries a node, which is rounded in specimens from Scania (Westergård 1946) and elongate in the new specimens from the allochthon (Fig. 28G–I). The border is wider than in the cephalon. None of the pygida at hand show traces of a median postaxial furrow, such as are occasionally seen in non-Scandinavian specimens (see below).

Populations from Australia, Siberia, Salair, Kazakhstan and large collections from South China (the latter deriving from different stratigraphical levels and including different ontogenetic stages) agree well with the Swedish material but display a wider range of variations. Of particular interest are two partly exfoliated pygidia from China, showing faint traces of an incomplete median postaxial furrow (Peng & Robison 2000, fig. 46:12–13). Egorova *et al.* (1982, pl. 18, fig. 5) figured a complete specimen of *H. brevifrons* from Siberia with a fully developed median postaxial furrow. A pygidium from Kazakhstan illustrated by Ergaliev & Ergaliev (2008, pl. 9, fig. 10) likewise has a median postaxial furrow. However, the population from the Indian Himalaya, described by Peng *et al.* (2009b), is different from that of all the aforementioned regions. In the cephalon, the glabella is proportionally longer and tapers only moderately. It agrees with regard to the overall shape of *H. brevifrons* and the cephalic border is also narrower than in the pygidium. All pygidia from the Indian Himalaya have a median postaxial furrow, only occasionally seen in China, Siberia and Kazakhstan, and never observed in Scandinavian material.

Hypagnostus clipeus **Whitehouse, 1939**

Figure 31M

1939 *Hypagnostus clipeus* sp. nov. Whitehouse, p. 263, pl. 25, figs 25–26.
1971 *Hypagnostus clipeus* Whitehouse; Hill, Playford & Woods, pl. 9, fig. 5.
1979 *Hypagnostus clipeus* Whitehouse; Öpik, p. 67, textfig. 18, pl. 5, figs 1, 7.
pars 2000 *Hypagnostus parvifrons* (Linnarsson); Peng & Robison, p. 60, fig. 45:4 & 6–11.
2007 *Hypagnostus parvifrons* (Linnarsson); Jago & Cooper, p. 475, fig. 2G–H, J–P.
2014 *Hypagnostus* aff. *clipeus* Whitehouse; Weidner & Nielsen, p. 50, fig. 23A.

Holotype. – Complete specimen, UQF3397, figured by Whitehouse (1939, pl. 25, fig. 25) and refigured by Hill *et al.* (1971, pl. Cm 9, fig. 5). It was collected from the V-Creek Limestone (*Doryagnostus deltoides* Zone) of Queensland, Australia. The *D. deltoides* Zone corresponds approximately to the *P. punctuosus* Zone of Scandinavia.

Material and occurrence. – One pygidium from the *A. atavus* Zone at Granberget. The only other find in Scandinavia is a pygdium from the same zone on Bornholm, Denmark (Weidner & Nielsen 2014). Elsewhere, *H. clipeus* occurs in the *Doryagnostus deltoides* and *Goniagnosti nathorsti* zones of the Undillan Stage, Australia (Hill 1971; Öpik 1979), China (Peng & Robison 2000) and on Antarctica in the *A. atavus* Zone (Jago & Cooper 2007).

Description. – The pygidium of *H. clipeus* is similar to that of *H. parvifrons*. In *H. clipeus,* the border is of even width all around, or almost so. The axis does not reach the border and a postaxial furrow of variable length may be present. The axial node is elongate (Fig. 31M; Öpik 1979, pl. 5, figs 1, 7, textfig. 18; Weidner & Nielsen 2014, fig. 23A; Peng & Robison, fig. 45:6–11; Jago & Cooper 2007, fig. 2K–P). In *H. parvifrons*, the border becomes considerably wider rearward and expands forward behind the axial tip and the axis bears a stout but rounded node. These are constant features of *H. parvifrons* and *H. mammillatus* observed throughout Scandinavia (Figs. 31 & 30; Høyberget & Bruton 2008, pl. 4I–L) and, hence, we recognize *H. clipeus* as a different species, contrary to Peng & Robison (2000) and Jago & Cooper (2007).

Hypagnostus lingula **(Grönwall, 1902)**

Figure 29A–W

pars 1902 *Agnostus lingula* n. sp. Grönwall, p. 73, pl. 1, fig. 15; *non* fig. 14 = *Svenax pusillus* (Tullberg, 1880).
1935 *Agnostus parvifrons* Linrs. var. Asklund & Thorslund, p. 107, pl. 1, figs 3, 4.
1946 *Hypagnostus truncatus* (Brögger) Forma 2 Westergård, p. 47, pl. 5, figs 13–19.
2008 *Hypagnostus lingula* (Grönwall); Høyberget & Bruton, p. 39, pl. 5, figs I–N.
2016 *Hypagnostus lingula* (Grönwall); Mannelqvist, p. 17, fig. 8:4, 8:6.

Lectotype (designated by Høyberget & Bruton 2008). – Pygidium, MGUH 153, originally figured by Grönwall (1902, pl. 1, fig. 15), refigured by Høyberget & Bruton (2008, pl. 5N). It derives from the *P. punctuosus* Zone in the Alum Shale Formation at Borggård, Øleå, Bornholm, Denmark. As pointed out by Høyberget &

Bruton (2008), the two detached cephala described by Grönwall (1902, p. 73, pl. 1, fig. 14) as *H. lingula* do not belong to this species; see remarks below.

Material and occurrence. – More than one hundred cephala and pygidia were collected for closer study from the *A. atavus* Zone at Fjällbränna, Strömnäs and Granberget, where *H. lingula* is the dominant species. No other agnostoid has been found in such quantities in the Vilhelmina area. In Sweden, the species is further known from the *A. atavus* Zone at Abborrfallet in northern Jämtland and from a boring at Motala, Östergötland (Asklund & Thorslund 1935; Westergård 1946). The species is very rare in southern Scandinavia. A single pygidium has been found at As Hoved, Denmark, in an ice-rafted boulder with provenance from Västergötland (collection TW). From Bornholm, Denmark, only the lectotype pygidium from the *P. punctuosus* Zone is known (Grönwall 1902), and the species has not been recorded from Scania, otherwise renowned for its diverse agnostoid fauna. In southern Norway, the species has been described as abundant in the *A. atavus* Zone at various localities in autochthonous and allochthonous strata (Høyberget & Bruton 2008). *Hypagnostus lingula* is known only from Scandinavia.

Remarks. – *Hypagnostus lingula* has recently been thoroughly described and illustrated by Høyberget & Bruton (2008), permitting identification of morphological details that distinguish this species. Their investigation was based on several hundred specimens from southern Norway. These authors also recognized the synonymy of *Hypagnostus truncatus* (Brøgger) Forma 2 *sensu* Westergård (1946).

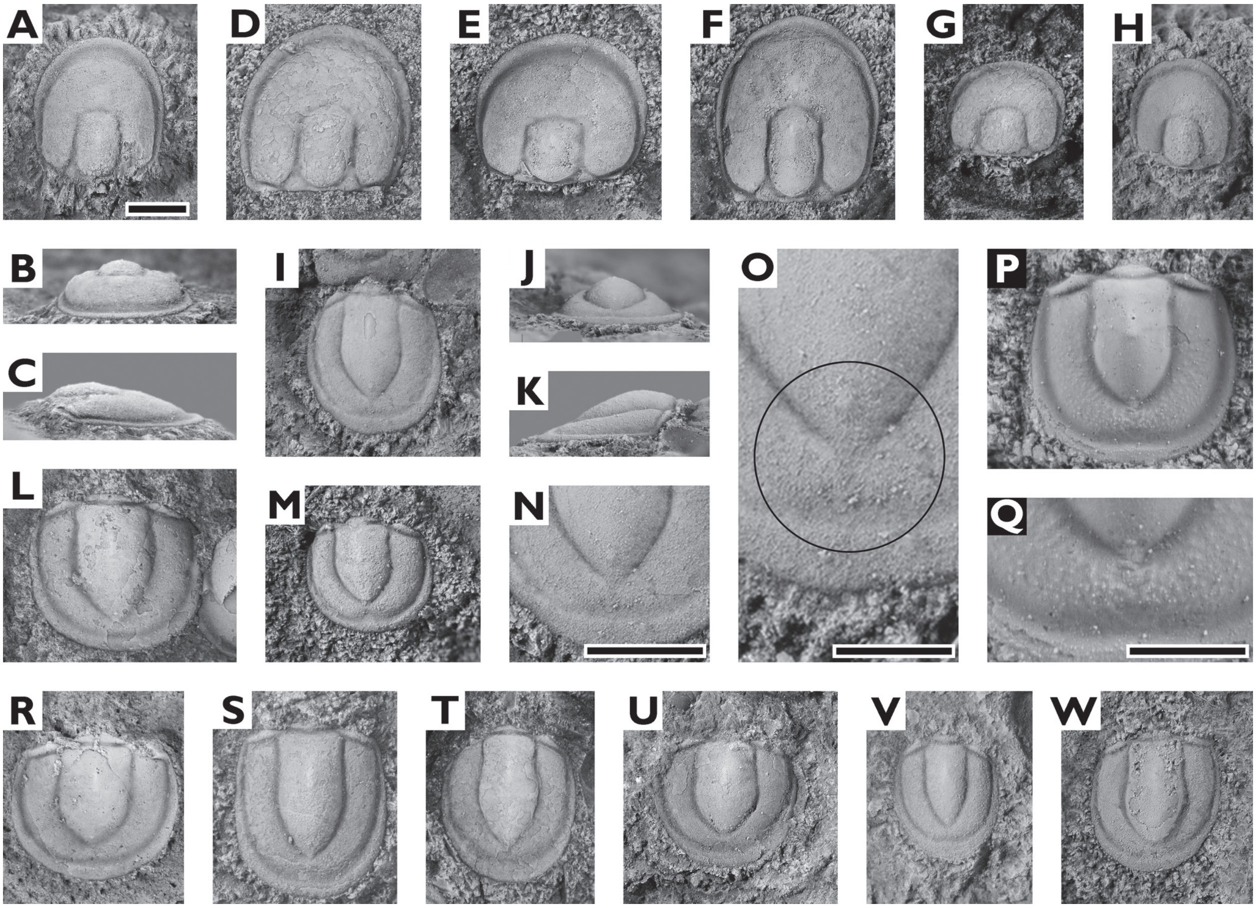


Fig. 29. **Hypagnostus lingula (Grönwall, 1902)**, *A. atavus* Zone. **A–H**, cephala. B, anterior and C, lateral views of A. F showing slight scrobiculation and a rare 'frontal recess'. PMU 29675, 29684, 29681/1, 29681/2, 29678/2, 29679/4. **I–W**, pygida. J, posterior and K, lateral views of I, N and O are close-up views of I, showing the post-axial ridge that separates the left from the right axial furrow and the terminal node. PMU 29680. P, the **lectotype** pygidium of *Hypagnostus lingula* (Grönwall, 1902) from the *P. punctuosus* Zone at Øleå, Bornholm, Denmark. MGUH 153. It was previously illustrated by Grönwall (1902, pl. 1, fig. 15). Q, showing the post-axial ridge. L–M, PMU 29673, 29683/2 and R–W, PMU 29672, 29685/1, 29678/1, 29679/1, 29677, 29686/2. A–C and V are from Strömnäs. D–K, M–O, S–U and W are from Fjällbränna. L and R are from Granberget. Scale bars A–M, P and R–W = 1 mm, N and Q = 1 mm, O = 0.5 mm.

The pygidium of *H. lingula* mostly has confluent pleural fields like a few other species. However, the lectotype from Bornholm, plus many of our new specimens, as well as material from Norway described by Høyberget & Bruton (2008), have a narrow and short ridge-like extension of the axis that in well-preserved specimens separates the left and the right axial furrows (best seen in Fig. 29N,O, Q). This is a unique feature not seen in any other agnostoid described from Scandinavia, in which the pygidial axis in species with confluent pleural fields is completely bounded by axial furrows. Few other specimens of *H. lingula* have confluent axial furrows (Fig. 29R, U), or show traces of a median postaxial furrow (Fig. 29I, M). The axis carries a small terminal node. Isolated cephala are difficult to distinguish from *H. truncatus*, which has a wide frontal recess that is only rarely seen in *H. lingula* (Fig. 29F). Furthermore, *H. lingula* is small, whereas a full-grown *H. truncatus* is large. A distinction between cephala of *H. lingula* and *H. frontosa* is otherwise impossible (see Weidner & Nielsen 2014). Overall, their proportions are the same and features such as smooth or slightly scrobiculated surfaces and anteriorly truncate or angulate glabellae occur in both species. In *H. parvifrons*, the glabella is expanded and rounded anteriorly, whereas in *H. lingula* it is parallel-sided and ending truncately or slightly angulate.

Grönwall (1902) assigned two detached cephala and one pygidium to *H. lingula*. The description of the cephala matches the illustrated specimen, i.e. glabella with distinct anteroglabella, basal lobes not united behind the glabella, and cheeks covered by radiating grooves. In *H. lingula*, however, the anteroglabella is effaced, the basal lobes unite behind the glabella (Fig. 29D–H), and the cheeks are smooth (Høyberget & Bruton 2008). The cephalon figured by Grönwall (1902, pl. 1, fig. 14) represents *Svenax pusillus*.

Hypagnostus mammillatus **(Brøgger, 1878)**

Figure 30A–I

1878 *Agnostus parvifrons* Linnarsson var. *mammillata* Brøgger, p. 72, pl. 5, figs 3a–d.
1946 *Hypagnostus parvifrons mammillatus* (Brögger); Westergård, p. 45, pl. 5, figs 2–4.
2009 *Hypagnostus mammillatus* (Brøgger); Weidner & Nielsen, p. 263, fig. 14C.
2008 *Hypagnostus mammillatus* (Brøgger); Høyberget & Bruton, p. 38, pl. 4, figs M–T.
2012 *Hypagnostus mammillatus* (Brøgger); Buchholz, p. pl. 1, fig. L.
2014 *Hypagnostus mammillatus* (Brøgger); Weidner & Nielsen, p. 46 (*cum syn.*), fig. 21E–G.
2016 *Hypagnostus mammillatus* (Brøgger); Mannelqvist, p. 17, fig. 8:1–3, 8:5.

Lectotype (designated by Høyberget & Bruton 2008). – Pygidium, PMO H2675, preserved in limestone, originally illustrated by Brøgger (1878, pl. 5, fig. 3b) and refigured by Høyberget & Bruton (2008, pl. 4R). The lectotype derives from the *P. punctuosus* Zone in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Material and occurrence. – Hypagnostus mammillatus is common in the *A. atavus* Zone at Fjällbränna, Djupdalsbäcken and Granberget as in most Cambrian provinces of Sweden (see e.g. Westergård 1946). For occurrences elsewhere, see Weidner & Nielsen (2014). The species ranges through the *A. atavus* and *P. punctuosus* zones, but is rare in the latter.

Remarks. – Hypagnostus mammillatus and *H. parvifrons* have identical cephala but are distinguished by the pygidium. *Hypagnostus mammillatus* has a variably inflated axis, a node placed closer to the center as the posteroaxis is slightly shorter than in *H. parvifrons* and a posterior border widening considerably behind the axis. The latter character cannot be seen in our new specimens, but see Weidner & Nielsen (2014), fig. 21C, D versus 21G. The differences between the two species must be assessed in lateral views (Fig. 30 H, *H. mammillatus*, versus K, *H. parvifrons*). In many specimens the axial node is broken off, leaving a scar much larger than the node itself (Fig. 30C).

Hypagnostus parvifrons **(Linnarsson, 1869)**

Figures 30J–L, 31A–L, N–R

1869 *Agnostus parvifrons* n. sp. Linnarsson, p. 82, pl. 2, figs 56, 57.
1946 *Hypagnostus parvifrons* (Linnarsson); Westergård, p. 45, pl. 4, figs 27–31.
1946 *Hypagnostus parvifrons cicatricosus* subsp. n. Westergård, p. 46, pl. 5, fig. 1.
1979 *Hypagnostus parvifrons* (Linnarsson); Neben & Krueger, pl. 115, figs 3, 4.
pars 2000 *Hypagnostus parvifrons* (Linnarsson); Peng & Robison, p. 60, fig. 45:1–3, 5; *non* fig. 45:4, 6–11 [= *H. clipeus* Whitehouse, 1939].
2004a *Hypagnostus parvifrons cicatricosus* Westergård; Buchholz, p. 508, pl. 1, figs 11, 12.
non 2007 *Hypagnostus parvifrons* (Linnarsson); Jago & Cooper, p. 475, fig. 2G–H, J–P [= *H. clipeus* Whitehouse, 1939].
2012 *Hypagnostus parvifrons* (Linnarsson); Buchholz, pl. 1, figs G–K.
2014 *Hypagnostus parvifrons* (Linnarsson); Weidner & Nielsen, p. 48 (*cum syn.*), figs 21C, D, 22P.
2014 *Hypagnostus cicatricosus* Westergård; Weidner & Nielsen, p. 45, fig. 21A, B.

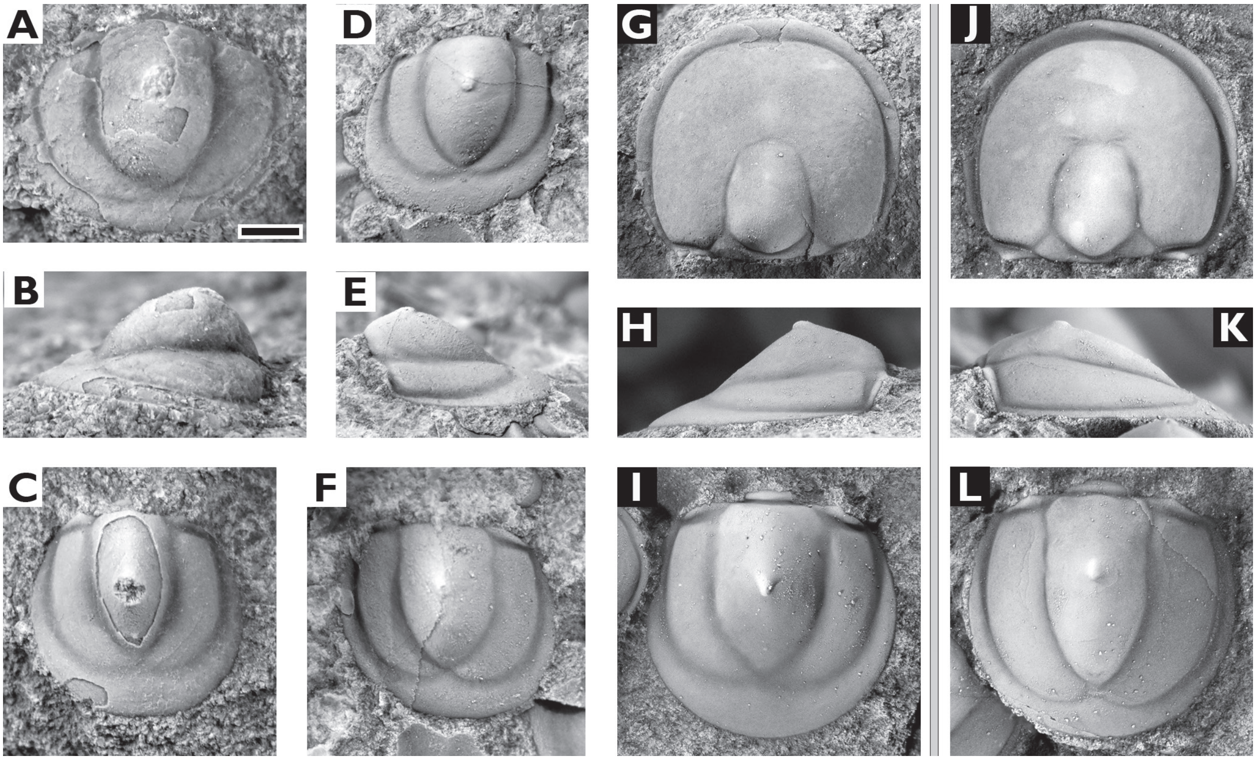


Fig. 30. ***Hypagnostus mammillatus* (Brøgger, 1878)**, *A. atavus* Zone. **A–B**, pygidium in dorsal and lateral view from Fjällbränna. PMU 37158. **C**, pygidium from Granberget. PMU 37154. **D–E**, pygidium in dorsal and lateral view and **F**, pygidium from Djupdalsbäcken. PMU 37159/1, 37159/2. **G–I** are a well-preserved cephalon and a pygidium in lateral and dorsal view from ice-rafted boulder, As Hoved, Denmark. PMU 34442/2 and PMU 34442/3. ***Hypagnostus parvifrons* (Linnarsson, 1869)**, *A. atavus* Zone. **J**, cephalon and **K**, **L** pygidium, from autochthonous strata at Vilske, Västergötland, shown for comparison with *H. mammillatus*. PMU 34440/2 and PMU 34440/1. Note the difference in the elevation of the pygidial axis, the position of the axial node and the width of the posterior border versus *H. mammillatus*. Scale bar = 1 mm.

Lectotype (designated by Westergård 1946). – Cephalon, SGU 4769, originally illustrated by Linnarsson (1869, pl. 2, fig. 56) and refigured by Westergård (1946, pl. 4, fig. 27) and Shergold & Laurie (1997, fig. 226:5a). The specimen derives from the upper part of the *A. atavus* Zone in the Alum Shale Formation at Hällekis, Kinnekulle, Västergötland, Sweden.

Paralectotype. – Pygidium, SGU 4768, from the same level as the lectotype, originally illustrated by Linnarsson (1869, pl. 2, fig. 57), refigured by Westergård (1946, pl. 4, fig. 28) and by Shergold & Laurie (1997, fig. 226:5b).

Material and occurrence. – Hypagnostus parvifrons is common in the *A. atavus* Zone at Abborrfallet, Högnäsån, Kvarnbäcken, Tåsjö church, Bellviks Hällan, Fjällbränna, Djupdalsbäcken, Stendalsbäcken, Dantas Mountain and Granberget. Kulling (1955) also listed the species from Skansholm, Ängesbäcken, Skikkisjö Mountain and Lubbträsk. Elsewhere it is a common species in nearly all Cambrian provinces of Scandinavia and it is known also from various countries outside Scandinavia; for distribution, see Weidner & Nielsen (2014). It ranges through the *A. atavus* and *P. punctuosus* zones (Høyberget & Bruton 2008).

Remarks. – Some cephala have ornamented cheeks showing shallow, irregularly radiating scrobicules (Fig. 31E–F). Weidner & Nielsen (2014) assigned such material to *Hypagnostus cicatricosus* Westergård, 1946. However, after renewed studies of large populations of several agnostoid species which display smooth as well as ornamented cheeks we no longer consider this feature as a valid character for separating species (see comments on *O. hybridus*). The figured specimens are assigned to *H. parvifrons* because the pygidial border widens posteriorly and shows the distinct forward projection characteristic for this species. The segmentation of the axis is effaced or indicated by very faint constrictions of the axis. The slightly elongated axial

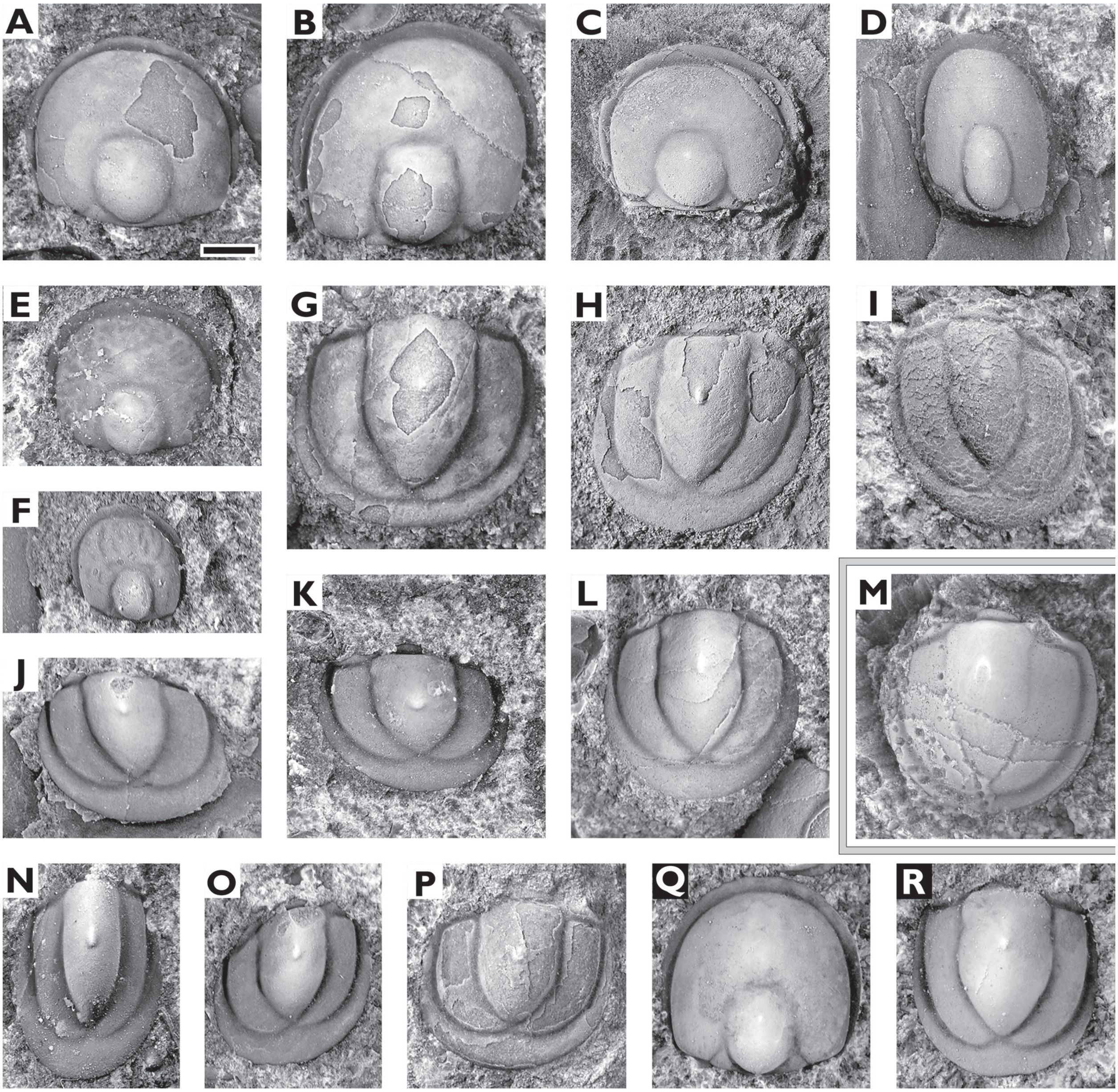


Fig. 31. ***Hypagnostus parvifrons*** **(Linnarsson, 1869)**, *A. atavus* Zone. **A–F**, cephala. PMU 37156a/1, 37156a/2, 29708, 37161/1, 37155, 37157. **G–L**, **N–P**, pygidia. PMU 37156b/1, 29709, 37164, 37160/1, 37161/3, 37156a/3, 37161/2, 37160/2, 37162. A–B, D, G, J–L, N–O are from Djupdalsbäcken, C and E are from Granberget, F is from Stendalsbäcken, H and P are from Fjällbränna, I is from Dantas Mountain. **Q–R**, a well-preserved cephalon and pygidium from St. Stolan on Billingen, Västergötland, shown for comparison. PMU 37083/1, 37083/3. ***Hypagnostus clipeus*** **Whitehouse, 1939.** from the *A. atavus* Zone on Granberget. **M**, pygidium, PMU 36411. Scale bar = 1 mm.

node is situated on M2, immediately in front of the F2 furrow (Fig. 31G, L, R). The cephalon is rounded, has a narrow border and border furrow and the glabella is rounded anteriorly with a weak node placed anterior of midlength. For comparison with *H. truncatus* and *H. lingula*, see remarks on these species.

Pygidia from China and Antarctica illustrated as *H. parvifrons* by Peng & Robison (2000) and Jago & Cooper (2007) lack the diagnostic traits of this species, i.e. a border considerably widening rearwards and expanding forward behind the axial tip. We consider their material as belonging to *H. clipeus* (see above).

Hypagnostus truncatus (Brøgger, 1878)

Figure 32A–S

1875 *Agnostus* sp. Brøgger, p. 579, pl. 25, fig. 1.
1878 *Agnostus truncatus* n. sp. Brøgger, p. 72, pl. 6, fig. 8.
1946 *Hypagnostus truncatus* (Brögger) forma 3 Westergård, p. 47, pl. 5, figs 20–23.

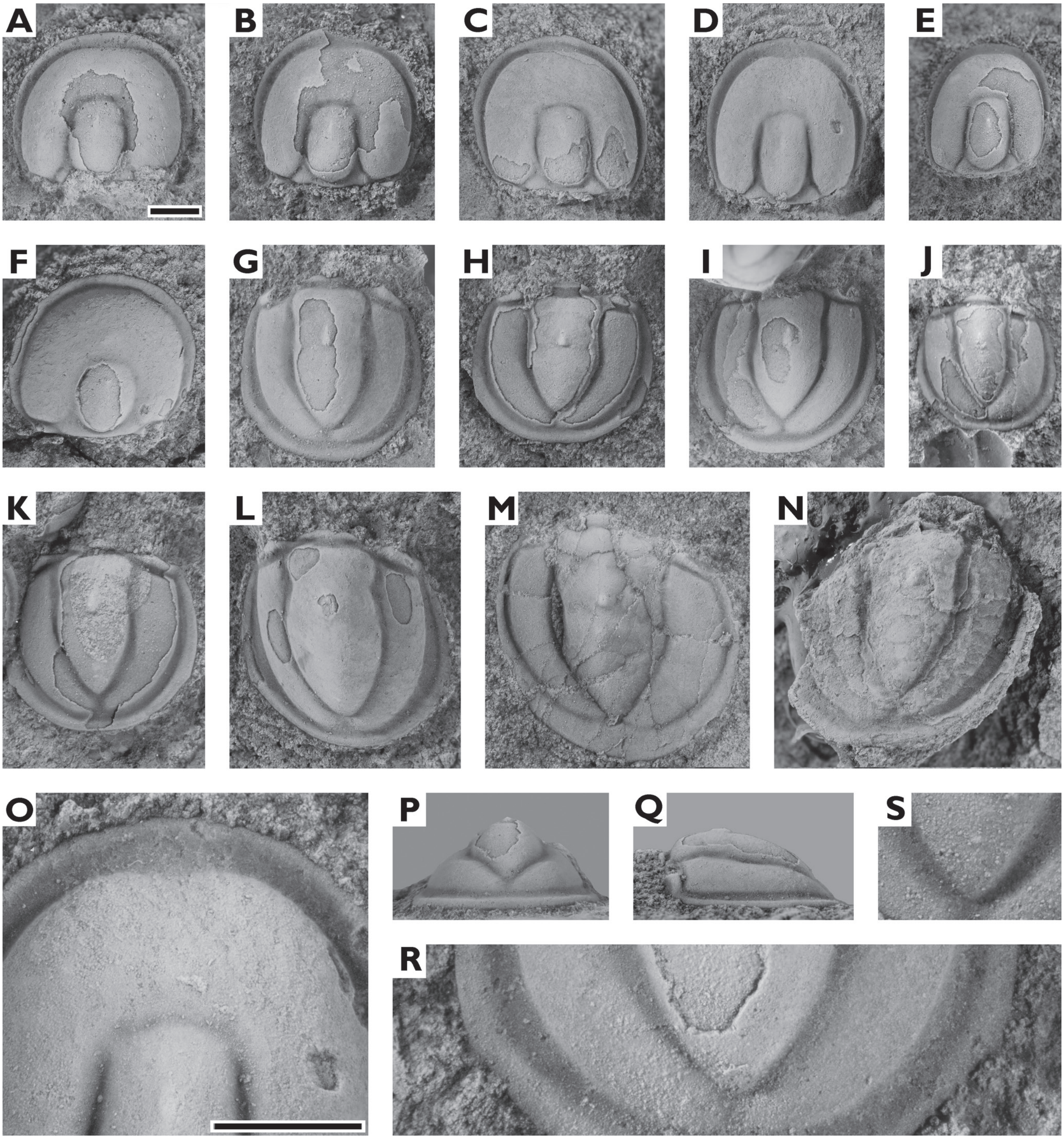


Fig. 32. ***Hypagnostus truncatus* (Brøgger 1878)**. All from the *A. atavus* Zone, except N, which is from the *P. punctuosus* Zone. **A–F**, **O**, cephala. O is close-up view of D, showing the 'frontal recess'. PMU 29694/2, 29694/3, 29695, 29696, 29704, 29701. **G–N**, **P-S**, pygidia. P is posterior, Q lateral and R close-up view of the lateral marginal swellings of G. S shows the terminal node of K. PMU 29698, 29703/1, 29693/1, 37201, 29702/2, 29700, 26176/1, 29706. A–L are from Granberget, M is from Bellviks Hällan and N is from Strömnäs. Scale bars = 1 mm. Scale bar in A is the same for A–N and P–Q, scale bar in O is the same for O, R–S.

1994 *Hypagnostus brevifrons* (Angelin); Robison, fig. 15:1–3, 6 [reassigned to *H. truncatus* by Peng & Robison, 2000, p. 63].

2008 *Hypagnostus truncatus* (Brøgger); Høyberget & Bruton, p. 41, pl. 5, figs O–X.

2014 *Hypagnostus truncatus* (Brøgger); Weidner & Nielsen, p. 49 (*cum syn.*), fig. 22Q–T.

Holotype (OD). – Cephalon, PMO 27156, originally illustrated by Brøgger (1875, pl. 25, fig. 1; 1878, pl. 6, fig. 8), re-illustrated by Høyberget & Bruton (2008, pl. 5, fig. O). The holotype originates from the *P. punctuosus* Zone in the Alum Shale Formation at Øksna, Norway.

Material and occurrence. – The species has been collected from the *A. atavus* Zone at Granberget and a few specimens derive from the *P. punctuosus* Zone at Strömnäs. It has further been collected from the *A. atavus* Zone at Högnäsån and Bellviks Hällan on the Tåsjö Mountain, and it was reported from Siljeåsen and the Tjärnmyr Mountain in northern Jämtland by Westergård (1946). In Denmark, it occurs at the same level on Bornholm (Weidner & Nielsen 2014) and it has also been found in ice-rafted boulders at As Hoved with provenance from Västergötland, likewise from the *A. atavus* Zone (collection TW). In southern Norway, it is reported as common in the *P. punctuosus* Zone (Høyberget & Bruton 2008). Where present, *H. truncatus* generally occurs in large numbers. The species is known with certainty only from Scandinavia. Illustrated specimens from Avalonian Canada (Hutchinson 1962), Avalonian Great Britain (Lake 1906) and Siberia (Egorova *et al.* 1982) are not *H. truncatus* (Høyberget & Bruton 2008; Weidner & Nielsen 2014).

Remarks. – Based on new topotype material, *H. truncatus* was thoroughly described and illustrated by Høyberget & Bruton (2008), and we refer the reader to their description; however, see also Weidner & Nielsen (2014). Nearly all of our new cephala have the characteristic wide and deep border furrow with a 'frontal recess', a feature separating *H. truncatus* from other *Hypagnostus* species (Høyberget & Bruton 2008). The pygidia are identified by their wide border and border furrow, both widest just opposite of a pair of lateral marginal swellings. The axis occasionally has a tiny terminal node.

Both *H. parvifrons* and *H. frontosa* lack the wide and deep border furrow and the frontal recess of *H. truncatus*. The posteroglabella of *H. parvifrons* is expanded and rounded anteriorly, whereas in *H. truncatus* it is parallel-sided and is truncated or slightly angulate anteriorly. In *H. frontosa*, the posteroglabella is slightly expanded or parallel-sided, and is similarly truncate as in *H. truncatus*. In one specimen from Denmark, a weak frontal recess of the border furrow is observed (Weidner & Nielsen 2014, fig. 22A). *Hypagnostus lingula* is smaller than *H. truncatus*, but otherwise isolated cephala are difficult to distinguish as the border furrow in *H. lingula* also is wide and may display a frontal recess (Fig. 30A, D). Regarding the pygidium, the strongly widened and flat posterior border in *H. parvifrons* distinguishes it from *H. truncatus*, *H. frontosa* and *H. lingula*. *Hypagnostus lingula* generally has confluent pleural fields. A narrow and short ridge-like extension of the axis separates the left from the right axial furrow in well-preserved specimens (Fig. 30H–O; Høyberget & Bruton 2008, pl. 5M, N). *Hypagnostus frontosa* pygidia differ from *H. truncatus* in having a narrow border furrow and a wide, flat border, and in lacking lateral marginal swellings.

Genus *Tomagnostella* Kobayashi, 1939

Type species (OD). – *Agnostus exsculptus*, Angelin, 1851, from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, Andrarum, Scania, Sweden.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – From the Miaolingian of Scandinavia, four species nowadays assigned to *Tomagnostella* were treated by Westergård (1946), viz. *Hypagnostus nepos* (Brøgger, 1878) from the *G. nathorsti* Zone, *Hypagnostus exsculptus* (Angelin, 1851) from the lower part of the *L. laevigata* Zone and *Hypagnostus sulcifer* (Wallerius, 1895) and *Hypagnostus denticulatus* Westergård, 1946 from the upper part of the *L. laevigata* Zone. *Tomagnostella sulcifera integra* (Wallerius, 1895) differs from the main form only by lacking scrobiculation on the cephalon, which no longer is considered of taxonomic value (cf. Peng & Robison 2000). *Tomagnostella sulcifera* and *T. denticulata* are ranked as separate species by most authors, whilst opinions are more divided concerning *H. nepos* (Brøgger, 1878) and *H. exsculptus* (Angelin, 1851). Westergård (1946), Öpik (1979), Egorova *et al.* (1982), Tortello (2009, 2011) and Høyberget & Bruton (2008) retained *T. nepos* and *T. exsculpta* as separate species, whereas Robison (1988), Pratt (1992), Peng & Robison (2000) and Ergaliev & Ergaliev (2008) synonymized *T. nepos* with *T. exsculpta*, and we agree with them (see remarks below).

Tomagnostella exsculpta (Angelin, 1851)

Figure 33A–N, Q–U

pars 1851 *Agnostus exsculptus* n. sp. Angelin, p. 7, pl. 6, fig. 8, cephalon only [pygidium = cephalon *G. nathorsti* (Brøgger, 1878)].
1878 *Agnostus parvifrons* Linnarsson var. *nepos* Brøgger, p. 72, pl. 6, fig. 2.
pars 1880 *Agnostus exsculptus* Angelin; Tullberg, p. 22, pl. 1, fig. 10.
1880 *Agnostus parvifrons* Linnarsson forma 3 Tullberg, p. 35, pl. 2, fig. 28.
pars 1902 *Agnostus exsculptus* Angelin; Grönwall, p. 53.
pars 1939 *Tomagnostella exsculpta* Angelin; Kobayashi, p. 150, [*Tomagnostella* erected].
pars 1946 *Hypagnostus exsculptus* (Angelin); Westergård, p. 50, pl. 5, fig. 35; *non* pl. 6, figs 1–5 [= new species of *Tomagnostella*].

1946 *Hypagnostus exsculptus geminus* subsp. n. Westergård, p. 52, pl. 6, fig. 6.
1946 *Hypagnostus nepos* (Brögger); Westergård, p. 47, pl. 5, figs 5–8.
1958 *Hypagnostus exsculptus* (Angelin); Pokrovskaya, p. 84, pl. 3, figs 10–12.
non 1959 *Tomagnostella exsculpta* (Angelin); Howell, p. 186, fig. 127:2a, b [= new species of *Tomagnostella*]; fig. 127:2c–d [= *Tomagnostella sulcifera*].
1970 *Hypagnostus exsculptus* (Angelin); Hajrullina, p. 15, pl. 1, fig. 3.
1977 *Hypagnostus exsculptus* (Angelin); Romanenko, p. 166, pl. 23, figs 15, 16.
1979 *Tomagnostella nepos* (Brögger; Westergård); Öpik, p. 73, pl. 67, fig. 5; textfig. 21.
1982 *Hypagnostus exsculptus* (Angelin); Egorova *et al.*, p. 72, pl. 42, fig. 6; pl. 46, fig. 4.
1982 *Hypagnostus nepos* (Brögger); Egorova *et al.*, p. 70, pl. 23, figs 1, 2, 13; pl. 27, fig. 16; pl. 41, figs 1, 2.
1982 *Hypagnostus nepos* (Brögger); Yang, pl. 2, figs 8, 9.
1988 *Tomagnostella exsculpta* (Angelin); Robison, 51, fig. 12:8–12.
1992 *Tomagnostella exsculpta* (Angelin); Pratt, p. 40, pl. 7, figs 16–18.
pars 1994 *Tomagnostella exsculpta* (Angelin); Bordonaro & Liñán, p. 112, pl. 2, figs 12–18; *non* figs 10–11 [= species of *Hypagnostus*].
non 1994 *Tomagnostella exsculpta* (Angelin); Rudolph, p. 138, pl. 7, fig. 15 [= new species of *Tomagnostella*].
1994 *Tomagnostella nepos* (Brögger); Rudolph, p. 140, pl. 7, fig. 16.
1995 *Tomagnostella exsculpta* (Angelin); Bordonaro & Banchig, p. pl. 1, figs 8, 9.
1997 *Tomagnostella exsculpta* (Angelin); Shergold & Laurie, p. 358, fig. 226:2a.
1997 *Tomagnostella exsculpta* (Angelin); Tortello & Bordonaro, p. 80, fig. 4.7, ?4.8, 4.9–4.13.
2000 *Tomagnostella exsculpta* (Angelin); Peng & Robison, p. 84 (*cum syn.*), fig. 69:1–26.
2003 *Tomagnostella* cf. *exsculpta*; Axheimer & Ahlberg, p. 149, fig. 7B–C.
2004 *Tomagnostella exsculpta* (Angelin); Weidner, Ahlberg, Axheimer & Clarkson, p. 44.
2008 *Tomagnostella exsculpta* (Angelin); Ergaliev & Ergaliev, p. 137, pl. 9, fig. 15–17, 19–22; pl. 16, figs 1–11; pl. 24, fig. 3.
non 2008 *Tomagnostella exsculpta* (Angelin); Høyberget & Bruton, p. 44, pl. 7, figs A–D [= new species of *Tomagnostella*].
2008 *Tomagnostella nepos* (Brøgger); Høyberget & Bruton, p. 45, pl. 6, figs O–V.
2009 *Tomagnostella nepos* (Brøgger); Tortello, p. 254, fig. 3A–H.
2009b *Tomagnostella exsculpta* (Angelin); Peng *et al.*, p. 27, fig. 16.
2010 *Tomagnostella nepos* (Brögger); Buchholz, pl. 2, figs 8, 9.
2011 *Tomagnostella nepos* (Brøgger); Tortello, p. 120, fig. 2L–T.

Lectotype (designated by Westergård 1946). – Cephalon, NRM Ar2007, originally illustrated by Tullberg (1880, pl. 1, fig. 10), refigured by Westergård (1946, pl. 5, fig. 35a–b) and Shergold & Laurie (1997, fig. 226:2a). The specimen derives from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – *Tomagnostella exsculpta* was found at the coast near Skansholm and in the banks of the Fjällbränna creek, where it is very common and associated with a fauna typical of the *G. nathorsti* Zone (*G. nathorsti*, *D. planicauda bilobatus*, *A. ferox*, *L. lundgreni* and *V. marginatus*). *Tomagnostella exsculpta* also occurs in the *G. nathorsti* Zone and the lower part of the *L. laevigata* Zone at Siljeåsen and at Karbäcken and Brattbäcken on the Tåsjö Mountain. It has been recorded previously [as *T. nepos*] from Västergötland, Scania (Westergård 1946) and southern Norway (Høyberget & Bruton 2008) and [as *T. exsculpta*] from Västergötland and Scania [lectotype only] (Westergård 1946; Weidner *et al.* 2004). Other records are from the *G. nathorsti* Zone of Australia (Öpik 1979), the lower part of the *L. laevigata* Zone of Siberia (Egorova *et al.* 1982; Pokrovskaya 1958), Kazakhstan (Ergaliev & Ergaliev 2008), the Turkestan range (Hajrullina 1970), Indian Himalaya (Peng *et al.* 2009b), and the Precordillera of Mendoza, Argentina (Tortello 2009, 2011). In China, the species turns up in the *P. punctuosus* Zone and ranges through the *G. nathorsti* Zone (Peng & Robison 2000). On Greenland, it is known from the higher parts of the *L. laevigata* Zone (Robison 1988) and in Laurentian Canada, it is reported from the *Cedaria minor* Zone along with agnostoids typical of the upper part of the *L. laevigata* Zone (Pratt 1992). Worldwide, the species thus has a long range from the *P. punctuosus* Zone to the upper part of the *L. laevigata* Zone.

Discussion. – As noted in the introductory remarks on the genus, some authors treat *T. nepos* and *T. exsculpta* as separate species, whereas others synonymized them, and the latter interpretation is adopted here. However, as a further complication, it appears that most of the sparse Scandinavian material hitherto assigned to *T. exsculpta* represents a new and as yet unnamed species. Below we outline the basis of these conclusions.

Only two of Angelin's six detached syntype cephala of *Agnostus exsculptus* were regarded by Tullberg (1880) as belonging to this species and one was illustrated (*ibid.*, pl. 1, fig. 10). Westergård (1946) concurred with this interpretation, except that he considered one of the discarded syntype cephala as possibly belonging to *Hypagnostus exsculptus* as well (*ibid.*, pl. 6, fig. 1, NRM Ar2006, 5.5 mm long). He designated the specimen previously illustrated by Tullberg as lectotype (Westergård 1946, pl. 5, fig. 35). The three syntype cephala of *exsculptus* are all from the Andrarum

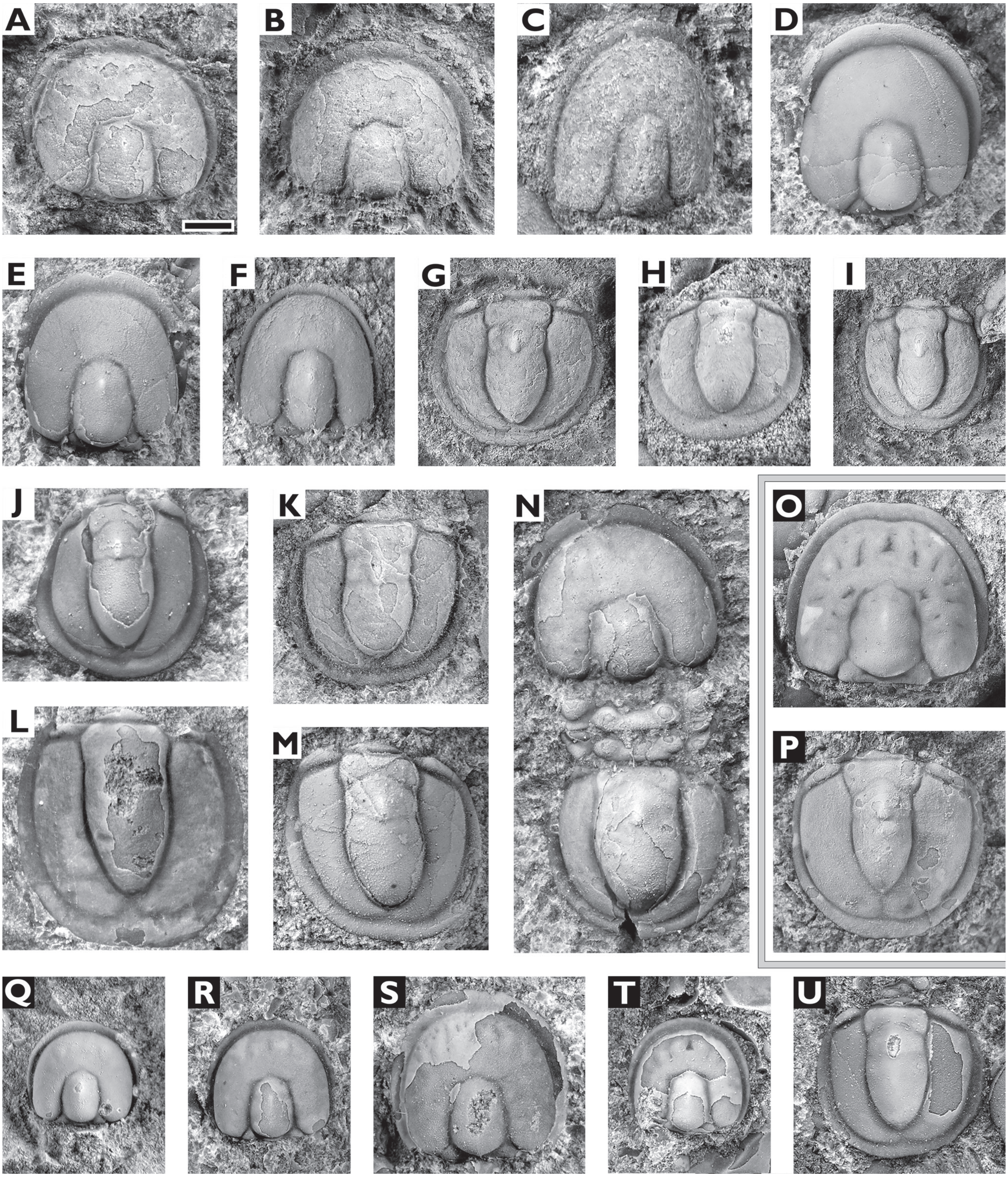


Fig. 33. ***Tomagnostella exsculpta*** **(Angelin, 1851)**, ***G.*** *nathorsti* Zone. **A–F** and **Q–T**, cephala. PMU 37169/1, 37169/3, 37171/1, 37168/2, 37168/3, 37165, 37151, 37228/1, 37228/2, 37229/2. G–**M** and **U**, pygidia. PMU 29691/8, 37172/2, 29691/7, 37167, 37172/1, 37246, 37168/1, 37227/2. **N** complete specimen. PMU 37173. A–C, G–I, K–L are from Fjällbränna, D–F and J, M–N are from Skansholm. Q–T, cephala and U, pygidium from autochthonous strata to compare with the Lapland material, *G. nathorsti* Zone. Q with smooth surface, R with weak scrobiculation, S and T with strong scrobiculation beneath the test and T indicates an incipient preglabellar furrow. Q is from Vilske, Västergötland and R–U are from Gislövshammar, Scania. ***Tomagnostella sulcifera*** **(Wallerius, 1895)**, from the upper part of the *L. laevigata* Zone at Vilske, Falbygden, Västergötland, to compare against *T. exsculpta*. **O**, cephalon. PMU 34319/1. **P**, pygidium. PMU 38335/2. Scale bar = 1 mm.

Limestone Bed at Andrarum in Scania. Westergård also had seven additional cephala collected from three different localities in Scania at his disposal of which one was figured (Westergård 1946, pl. 6, fig. 2). The lectotype, a small specimen (3.0 mm long), has a deep and narrow transglabellar furrow with an angular glabellar front and moderately scrobiculate cheeks. The two other cephala figured by Westergård are large specimens (5.5 and 5.6 mm long), with a truncate glabella and a straight and faint transglabellar furrow and more strongly scrobiculate cheeks. Three pygidia, possibly belonging to this species (7.0, 6.3 and 4.7 mm long), were also illustrated by Westergård (1946, pl. 6, figs 3–5). Høyberget & Bruton (2008, pl. 7, figs A–C) illustrated two large and one small cephalon (5.1, 6.0 and 3.2 mm long) from the same stratigraphical level in southern Norway that all look like the large cephala illustrated from Sweden. Høyberget & Bruton (2008) also assigned a pygidium (6.4 mm long), similar to the specimens illustrated by Westergård (1946, pl. 6, figs 3, 4). Thus, from Scandinavia only a very limited material referred to *T. exsculpta* has been described previously. From an ice-rafted boulder of Andrarum Limestone collected in northern Germany, Rudolph (1994) figured a small cephalon (2.1 mm long) showing all characteristics of the larger cephala illustrated from Sweden and Norway.

Illustrated cephala and pygidia from the Indian Himalaya (Peng *et al*. 2009b, fig. 16) and new material from Sweden (Fig. 33Q–T) allow us to unequivocally characterize *T. exsculpta* and that has convinced us that all material illustrated as *exsculpta* by Westergård (1946), Høyberget & Bruton (2008) and Rudolph (1994), except for the lectotype, represents an unnamed rare species of *Tomagnostella*. This species is well-described (as *T. exsculpta*) by Høyberget & Bruton (2008, pl. 7, figs A–D) and it includes the cephala and pygidia illustrated by Westergård (1946, pl. 6, figs 1–5) as well as the cephalon illustrated by Rudolph (1994, pl. 7, fig. 15). In comparison with *T. exsculpta* – *T. nepos*, the unnamed new species attains a larger maximum size, the cephalic F3 is usually effaced and the cephala are scrobiculate with 3–4 sizes of radiating scrobicules, and the pygidia have a slender and sharply pointed axis with a transverse sulcus near the tip. Høyberget & Bruton (2008, p. 44) note that 'F3 may be present and angular in smaller specimens', undoubtedly referring to the lectotype cephalon of *T. exsculpta*. However, of the two small cephala representing the new species, one lacks the furrow and the other has a straight furrow (Høyberget & Bruton 2008, pl. 7C; Rudolph 1994, pl. 7, fig. 15). This new species has not been found in the study area.

The complete specimen of *Agnostus parvifrons* Linnarsson var. *nepos* figured by Brøgger (1878) cannot be traced at PMO and Westergård's (1946) description and illustrations of the species were based on material from Sweden. The two illustrated cephala (Westergård 1946, pl. 5, figs 5, 7) from Scania (3.1 mm long) and Ångermanland (3.9 mm long), respectively, give the impression of a gently rounded transglabellar furrow, as in *H. parvifrons* or *H. mammillatus*. In fact, Westergård (1946) compared *H. nepos* with *H. parvifrons* and did not note any affinity with *H. exsculptus*. Topotype material of *T. nepos* from Krekling illustrated by Høyberget & Bruton (2008, pl. 6, figs O–R), including complete specimens (total length 6.0 and 6.5 mm), with cephala (2.9 and 3.5 mm long), shows, however, an angular transglabellar furrow as in the lectotype cephalon of *T. exsculpta*. Pygidia of *T. nepos* from Norway and Sweden are entirely similar (see Westergård 1946, pl. 5, figs 6, 8 [3.6 and 3.7 mm long] and Høyberget & Bruton 2008, pl. 6, figs Q–V [3.0, 3.5 and 2.9 mm long]).

Separation of *T. exsculpta* and *T. nepos* has been based solely on whether the cephalon is scrobiculate or smooth; see Westergård (1946), Öpik (1979), Egorova *et al.* (1982), Tortello (2009, 2011) and Høyberget & Bruton (2008). However, Robison (1988) and Peng & Robison (2000) observed variation in the surface ornamentation of the cheeks within large populations and they synonymized the two species, with *T. exsculpta* as the senior subjective synonym. Variation in the surface ornamentation is observed also in material collected by TW in Scania and Västergötland (Fig. 33Q–T). These cephala show a varying degree of scrobiculation and clearly bridge the smooth cephala of *T. nepos* with the furrowed lectotype cephalon of *T. exsculpta*. A recent publication on a fauna from the Indian Himalaya (Peng *et al.* 2009b) illustrates cephala and pygidia as *T. exsculpta*. The three illustrated cephala (3.3, 3.0 and 3.3 mm long) comply in all cephalic characters with the lectotype cephalon of *T. exsculpta* and also with the topotype cephala of *T. nepos* except for the lack of cephalic ornamentation (compare Peng *et al*. 2009b, fig. 16:4–6 versus Westergård 1946, pl. 5, fig. 35 and Høyberget & Bruton 2008, pl. 6, figs O–R). Illustrated pygidia (3.1, 3.0 and 4.2 mm long) from India resemble *T. nepos* as well (Peng *et al*. 2009b, fig. 16:7–12 versus Høyberget & Bruton 2008, pl. 6, figs Q–V). We conclude that *T. exsculpta* and *T. nepos* agree in size and morphological features and represent one species, having variably smooth, moderately or distinctly scrobiculate cephalic cheeks (Fig. 33Q–T).

Our cephala and pygidia from Lapland are sampled mostly from weathered limestone and any cephalic surface ornamentation that may have existed is not preserved. The specimens compare well with the Swedish and Norwegian material described as *T. nepos* by Westergård (1946) and Høyberget & Bruton (2008). The only illustrated cephala of *T. exsculpta* with cephalic scrobiculation are the lectotype and those published by Peng *et al*. (2009b). However, new material collected by us at Gislövshammar, Scania, includes three cephala of *T. exsculpta* with cephalic scrobiculation (Fig. 33R–T). They show the presence of shallow, widely spaced, radiating furrows as seen in the lectotype and the material from the Himalaya. In front is a triangular, deep depression. Cephala with a smooth surface from Norway (Høyberget & Bruton 2008, pl. 6O) and China (Peng & Robison 2000, fig. 69.3) and a cephalon with scrobiculate surface from Himalaya (Peng *et al*. 2009b, fig. 16.6) show the same depression.

Tomagnostella sulcifera (Wallerius 1895) differs in the cephalon from *T. exsculpta* in having a slightly wider glabella, distinct contrictions at F1 and F2, and M2 is bowed out laterally (Fig. 33O; Westergård 1946, pl. 6, figs 7[lectotype] & 10; Peng & Robison 2000, fig. 70:1-7). In the pygidium, the axis is shorter than in *T. exsculpta*, F1 and F2 are distinct, and the pleural fields are separated by a postaxial furrow (Fig. 33P; Peng & Robison 2000, fig. 70:8-10). In *T. exsculpta* the axis reaches the border or is connected with the border by a recess of the border of variable length (Fig. 33H–I, L).

Genus *Doryagnostus* Kobayashi, 1939

Type species (OD). – *Agnostus incertus* Brøgger, 1878, from the *P. punctuosus* Zone, Alum Shale Formation at Krekling, Oslo Region, Norway.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Two species, *D. incertus* (Brøgger, 1878) and *D. deltoides* Robison, 1978, occur in the Miaolingian of Scandinavia.

Doryagnostus deltoides Robison, 1978

Figures 34A–H (pygidium only), K–A', 35H

pars 1936 *Euagnostus opimus* sp. nov. Whitehouse, p. 87, pl. 8, fig. 10; *non* figs 11–12.
1971 *Euagnostus opimus* Whitehouse; Hill, Playford & Woods, pl. 9, fig. 4.
1978 *Doryagnostus deltoides* n. sp. Robison *in* Jell & Robison, p. 7, pl. 2, figs 7–9, 12.
pars 1979 *Euagnostus opimus* Whitehouse; Öpik; p. 75, only pl. 13, fig. 1.
1979 *Doryagnostus notalibrae* sp. nov. Öpik, p. 84, pl. 19, figs 1–4; pl. 21, figs 1–3.
1979 *Doryagnostus* sp. aff. *notalibrae* Öpik, p. 86, pl. 21, figs 5–6.

Holotype (OD). – Cephalon, UQF69624, figured by Jell & Robison (1978, pl. 2, fig. 9). It was collected from the Currant Bush Limestone (*P. punctuosus* Zone) in Queensland, Australia.

Material and occurrence. – Three pygidia were found in the *A. atavus* Zone at Granberget, Lapland. One cephalon derives from the *P. punctuosus* Zone at Brantevik, Scania. Eight cephala and pygidia were collected from the *P. punctuosus* Zone at Munkesten on Hunneberg in Västergötland, and five cephala and pygidia are from ice-rafted boulders at Ulbjerg and As Hoved, Jutland, Denmark. The boulder material is from the upper part of the *A. atavus* Zone and originates from Västergötland. Elsewhere, the species is reported only from the *E. opimus* and *P. punctuosus* zones of Queensland, Australia, i.e. from the same stratigraphical levels as in Sweden.

Remarks. – Our figured specimens match completely the diagnostic traits of this species emphazied by Jell & Robison (1978) and Öpik (1979). The cephala (Figs 34A, B&D, E&G; 35H) have a distinct deltoid area, the transglabellar furrow curve forward, and in the pygidium, the axis is gently downsloping towards the median postaxial furrow (Fig. 34L, O, R). The overall shape of the cephalon with an anteroglabella that is slightly wider than long and tapering to a point, and the position of the cephalic node, are shared with *D. incertus*. The pygidia of the two species differ as *D. incertus* has an axis that is narrower and strongly tapering and depressed in its posterior part. Both species possess a pair of lateral pygidial spines located approximately level with the tip of the axis.

We have observed intraspecific variability in the proportional width and length of the axis and the length of the median postaxial furrow in pygidia from Australia and Scandinavia (cf. Jell & Robison 1978; Öpik 1979; Fig. 34).

Associated cephala of *O. hybridus* (Fig. 34H1, J) can best be distinguished from those of *D. deltoides* (Fig. 34A, B, E) in the overall shape of the shield. In both *D. deltoides* and *D. incertus*, the greatest cephalic width is in front of the transglabellar furrow, in *O. hybridus* it is behind. Further, in *O. hybridus* the anteroglabella is slightly longer than wide and not wider than long as in *D. deltoides*.

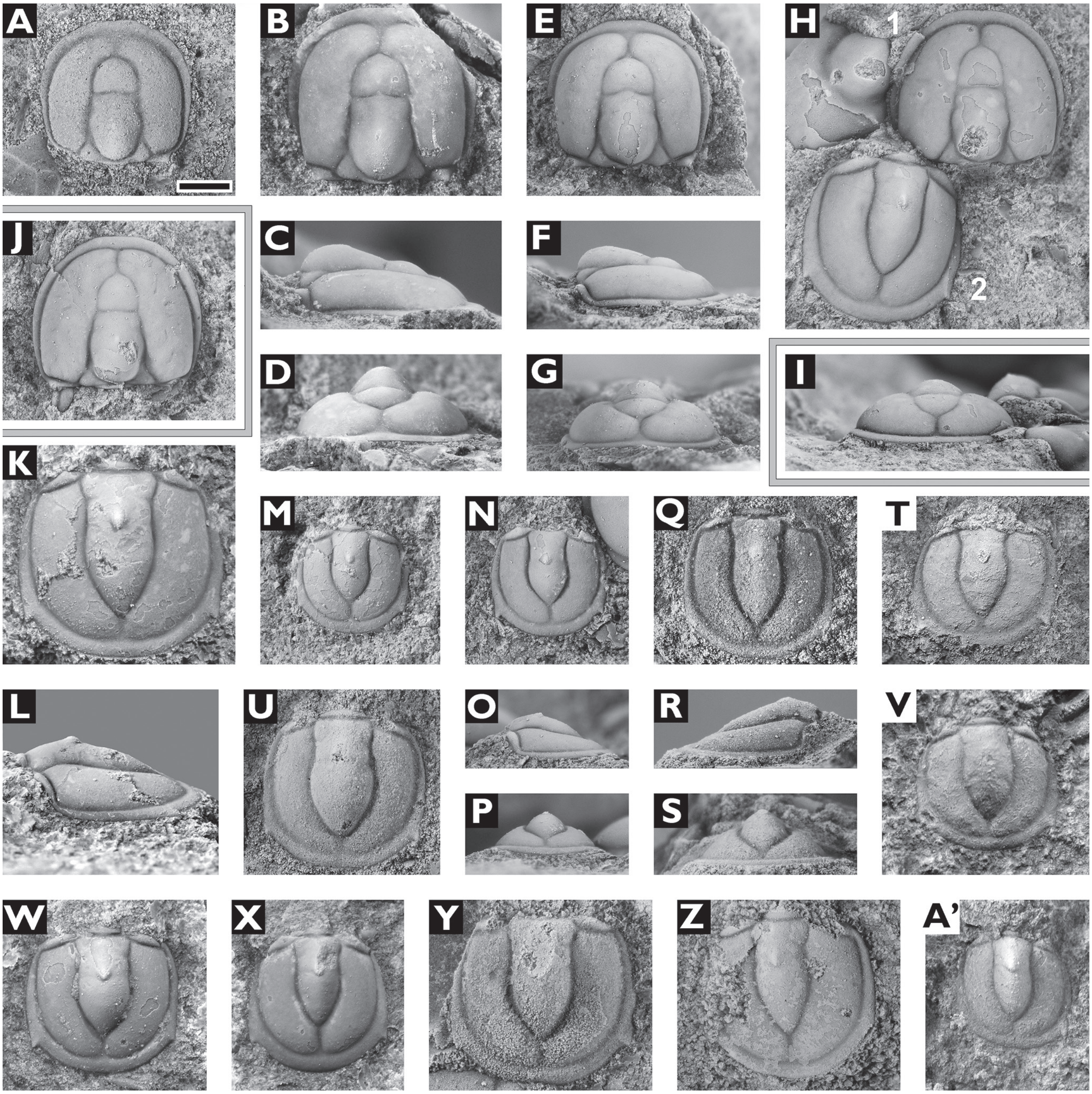


Fig. 34. ***Doryagnostus deltoides*** **Robison, 1978**. Only the pygidia T, V and A' are from the study area in Lapland. As this is the first record of this species from Scandinavia, specimens from other regions of Sweden are illustrated as support for the description. **A–G**, three cephala in dorsal, lateral and anterior views. A is from the *P. punctuosus* Zone at Munkesten, Västergötland. PMU 38340. B–D and E–G are from ice-rafted boulders, As Hoved, Denmark, representing the upper part of the *A. atavus* Zone. PMU 38348, 38349. **H2**, **K–A'**, are pygidia, partially in dorsal, lateral and posterior views. H2, K–P and W–X, are from ice-rafted boulders, As Hoved, Jutland, Denmark. PMU 38347/2, MGUH 34044, PMU 38336, PMU 38346, MGUH 34045, MGUH 34046. Q–S, U and Y are from Munkesten, Västergötland. PMU 38343, 38342, 38344/1. Z is from an ice-rafted boulder found at Ulbjerg, Jutland, Denmark, representing the upper part of the *A. atavus* Zone. PMU 38355/1. T, V and A' are from the *A. atavus* Zone at Granberget near Vilhelmina, Lapland. PMU 29703/3, 37202, 37131/1. ***Onymagnostus hybridus*** **(Brøgger, 1878)**, **H1, I–J**, cephalon shown in different views for comparison with the illustrated cephala of *D. deltoides*. The specimens have been collected from ice-rafted boulders at As Hoved, Denmark, representing the upper part of the *A. atavus* Zone. PMU 38347/1. I–J, PMU 38351. Scale bar = 1 mm.

Doryagnostus incertus (Brøgger, 1878)

Figure 35A–G, I–O

1878 *Agnostus incertus*, n. sp. Brøgger, p. 70, pl. 6, figs 4a, b.
1880 *Agnostus incertus* Brögger; Tullberg, p. 19, pl. 1, fig. 6a, b.
1902 *Agnostus incertus* Brögger; Grönwall, p. 52.
1907 *Agnostus incertus* Brögger; Lake, p. 29, pl. 3, figs 1–3.
1929 *Agnostus incertus* Brøgger; Strand, p. 344.
1935 *Agnostus incertus* Brögger; Asklund & Thorslund, pl. 1, figs 9, 10.
1939 *Doryagnostus incertus* (Brögger); Kobayashi, p. 148 [*Doryagnostus* erected].
1946 *Doryagnostus incertus* (Brögger); Westergård, p. 83, pl. 12, figs 20–23; pl. 13, figs 1–3.
1962 *Doryagnostus incertus* (Broegger); Hutchinson, p. 87, pl. 10, figs 9–11.
1971 *Doryagnostus magister* (Whitehouse); Hill, Playford & Woods, pl. 9, fig. 7.
1977 *Doryagnostus incertus* (Brögger); Zhou, Liu, Meng & Sun, p. 111, pl. 36, figs 20, 21.
1978 *Doryagnostus incertus* (Brøgger); Robison, p. 7, pl. 2, figs 1, 2, 8.
1979 *Doryagnostus incertus* (Brögger); Neben & Krueger, pl. 117, fig. 15.
1979 *Doryagnostus magister* (Whitehouse); Öpik, p. 83, pl. 17, figs 4–6; pl. 18, figs 1–5; pl. 20, figs 1–4; textfig. 24.
1985 *Doryagnostus magister* (Whitehouse); Xiang & Zhang, p. 71, pl. 19, figs 1–5.
1990 *Doryagnostus incertus* (Brøgger); Nikolaisen & Henningsmoen, p. 59, figs 2, 6H–M.
1990 *Doryagnostus incertus* (Brögger); Shergold, Laurie & Sun, p. 80, fig. 13:7.
1991 *Doryagnostus incertus* (Brögger); Yang *et al*., p. 115, pl. 6, figs 3–6.
1994 *Doryagnostus incertus* (Brögger); Rudolph, p. 141, pl. 2, figs 5–7.
1997 *Doryagnostus incertus* (Brögger); Shergold & Laurie, p. 359, fig. 228:1a, b.
2000 *Doryagnostus incertus* (Brøgger); Peng & Robison, p. 59, fig. 44.
2003 *Doryagnostus incertus* (Brögger); Axheimer & Ahlberg, p. 144, fig. 4E.
2004 *Doryagnostus incertus* (Brögger); Weidner, Ahlberg, Axheimer & Clarkson, fig. 3D, E.
2008 *Doryagnostus incertus* (Brøgger); Høyberget & Bruton, p. 27, pl. 2, figs M–O.

Lectotype (designated by Nikolaisen & Henningsmoen 1990). – Pygidium, PMO 28200, originally illustrated by Nikolaisen & Henningsmoen (1990, fig. 2a), refigured by Shergold & Laurie (1997, fig. 228:1b). The specimen derives from the *Paradoxides rugulosus* Zone (now *P. punctuosus* Zone) in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Paralectotypes. – Cephalon, PMO H2646, and pygidium on the same piece of shale, PMO H2646, from the same level as the lectotype, illustrated by Nikolaisen & Henningsmoen (1990, fig. 2b, c) and Shergold & Laurie (1997, fig. 228:1a).

Material and occurrence. – *Doryagnostus incertus* has been found in the *P. punctuosus* Zone at Stendalsbäcken, Strömnäs and Granberget and it has also been reported from the Skikkisjö Mountain by Kulling (1955). It is generally rare. On the Tåsjö Mountain, it occurs at Karbäcken and Kvarnbäcken and in northern Jämtland at Abborrfallet. In Västergötland, it has been reported from Munkesten, Hunneberg (Westergård 1946) and from a thin conglomeratic layer at Vilske, Mösseberget (Weidner *et al*. 2004). *Doryagnostus incertus* is known also from ice-rafted boulders of the same layer collected at As Hoved and Ulbjerg, Denmark (collection TW). Rudolph (1994) figured material from ice-rafted boulders collected in northern Germany. Except in Scania and on Bornholm, the species is uncommon. All reports are from the *P. punctuosus* Zone. In Norway, it occurs at many localities in the *P. punctuosus* Zone, but is everywhere rare. At two localities, it ranges into the *G. nathorsti* Zone (Brøgger, 1878; Høyberget & Bruton 2008). Outside Scandinavia, the species is reported from the *P. punctuosus* Zone of Avalonian Great Britain (Lake 1907) and Newfoundland (Hutchinson 1962). In Australia (Öpik 1979) and China (Peng & Robison 2000) it ranges into the *G. nathorsti* Zone.

Remarks. – *Doryagnostus incertus* has been described in detail by various authors, see especially Nikolaisen & Henningsmoen (1990) and Høyberget & Bruton (2008). The latter authors provided a discussion of the synonymy of *D. magister* Whitehouse, 1939 and *D. incertus* and we agree with their conclusions. Our own material is limited and poorly preserved and does not contribute anything new on this issue. The cephalon of *D. incertus* resembles *D. deltoides* Robison, 1978, from the *P. punctuosus* Zone of Australia but in that species the F3 furrow bends forward, the M3 is more pronounced and a deltoid area is developed (Fig. 35H). The cephalon of *D. incertus* resembles also that of *O. hybridus*, but in the latter the cheeks narrow strongly forwards (cf. Fig. 21A–C), while in *D. incertus* the cheeks narrow only moderately and in *O. hybridus*, the posteroglabella is laterally expanded, whereas it is slender and almost parallel-sided in *D. incertus*. In *O. hybridus*, the cephalon has its greatest width posteriorly, whereas in *D. incertus* it is in front of the transglabellar furrow. The pygidium of *D. incertus* resembles that of *G. nathorsti* but differs with regard to the shape of the axis, which is clearly segmented in *G. nathorsti*, while in *D. incertus* the furrows are effaced so the segmentation is only indicated by lateral constrictions.

Family Peronopsidae Westergård, 1936

Genus '*Diplorrhina*' Hawle & Corda, 1847

Type species. – Pek & Vaněk (1971) designated *Diplorrhina triplicata* Hawle & Corda, 1847, from the *Eccaparadoxides pusillus* Zone near Týřovice,

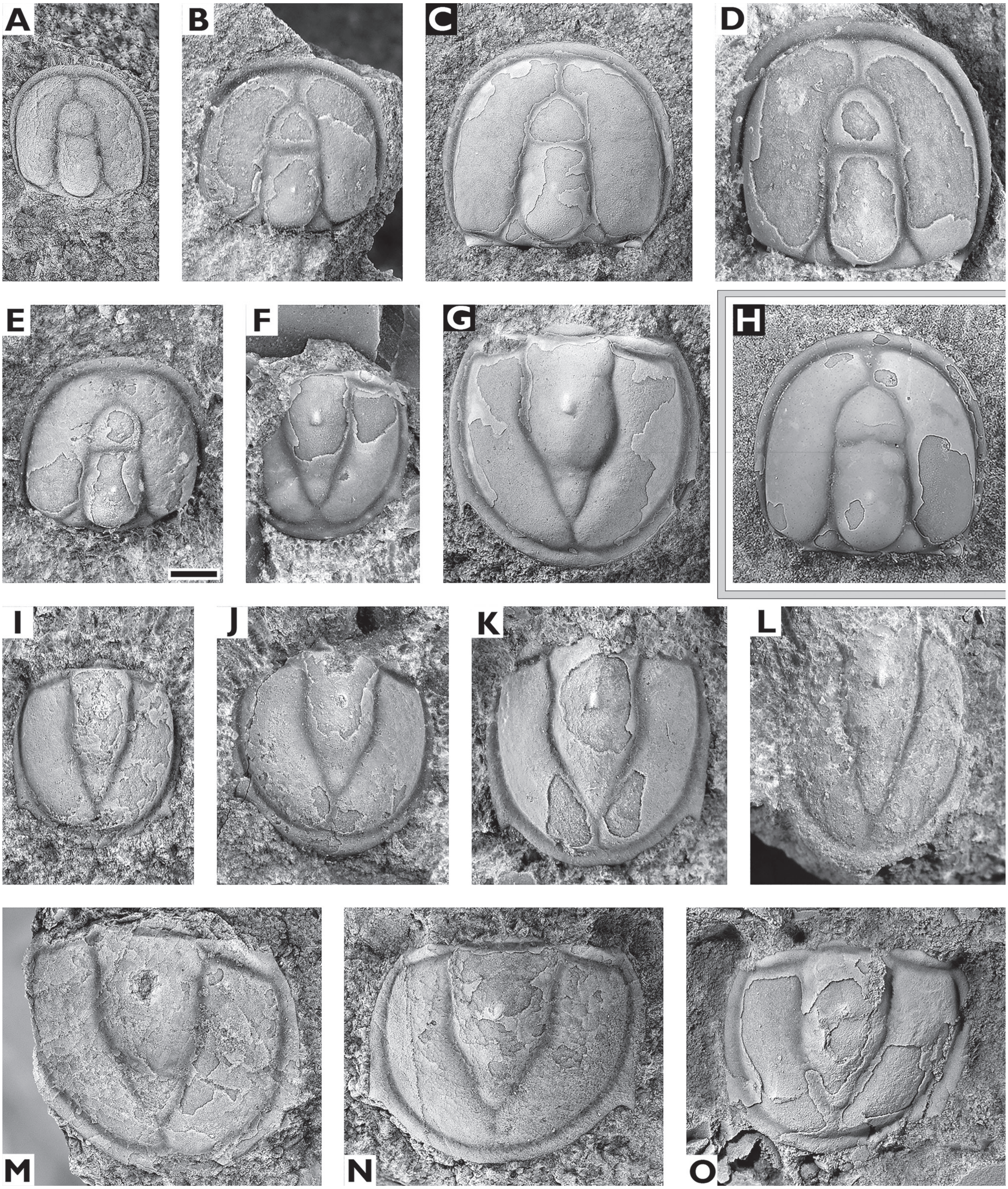


Fig. 35. ***Doryagnostus incertus*** **(Brøgger, 1878)**, *P. punctuosus* Zone. **A–E**, cephala. PMU 26233/2, 37176a, 26414/1, 37175, 37177. **F–G**, **I–O**, pygidia. PMU 37181a/1, 26414/4, 37179, 37178, 37180/1, 37174/1, 26235, 26233/1, 26237/1. PMU A, M–N are from Abborrfallet. B, D–E and I–K are from Granberget. F is from Stendalsbäcken, L from Strömnäs and O is from Kvarnbäcken. C and G show a well-preserved cephalon and pygidium from autochthonous strata at Brantevik, Scania, for comparison. ***Doryagnostus deltoides*** **Robison, 1978. H**, cephalon from Brantevik, Scania, *P. punctuosus* Zone, for comparison. PMU 37079. Scale bar = 1 mm.

Bohemia, Czechia, as the type species and this generic concept has been widely accepted. However, Rushton (1979) pointed out that *Diplorrhina sirius* Hawle & Corda, 1847 was designated as the type species already by Whitehouse (1936). That species is probably a synonym of *Peronopsis integra* (cf. Öpik 1967, p. 731) in which case *Diplorrhina* becomes a synonym of *Peronopsis*. Nonetheless, we here adopt the generally accepted interpretation of *Diplorrhina* as (erroneously) typified by *D. triplicata*, but refer to the genus as '*Diplorrhina*'. Either a new generic name should be introduced for the '*Diplorrhina*' species group or the designation of *D. sirius* as the type species should be overruled. Considering that the designation of type species made by Whitehouse (1936) has been overlooked by the majority of subsequent workers, the latter solution appears preferable as it stabilizes nomenclature.

Diagnosis. – See Robison (1994) and Shergold & Laurie (1997).

Remarks. – Three species of '*Diplorrhina*' have been recorded from the Miaolingian of Scandinavia, viz. '*D.*' *quadrata* (Tullberg, 1880), '*D.*' *cylindrica* (Westergård, 1946) and '*D.*' *depressa* (Westergård, 1946). In Fig. 36, cephala and pygidia of all three species are shown, illustrating the distinguishing features. Except for '*D.*' *quadrata*, the material is scarce, and for comparison, material from outside of the study area is also illustrated.

'*Diplorrhina*' *depressa* (Westergård, 1946)

Figure 36A–D

1946	*Peronopsis fallax depressa* subsp. n. Westergård, p. 37, pl. 2, figs 25, 26.
1962	*Peronopsis fallax* (Linnarsson) subsp. *P. depressa* Westergård; Hutchinson, p. 70, pl. 5, figs 8–11.
1979	*Peronopsis fallax depressa* Westergård; Rushton, p. 50, fig. 3B.
1994	*Diplorrhina depressa* (Westergård); Robison, p. 38.
1997	*Quadragnostus quadratus* (Tullberg); Buchholz, pp. 204, 243, pl. 19, fig. 10.
?2003	*Peronopsis fallax depressa* Westergård; Axheimer & Ahlberg, p. 145, fig. 4J.
2004a	*Quadragnostus depressus* (Westergård); Buchholz, p. 513, pl. 3, figs 1, 2.
2008	*Diplorrhina depressa* (Westergård); Høyberget & Bruton, p. 34, pl. 2, figs T–W.
2014	*Diplorrhina depressa* (Westergård); Weidner & Nielsen, p. 57, fig. 30A–L.

Holotype (OD). – Pygidium, SGU 4721, illustrated by Westergård (1946, pl. 2, fig. 26), collected from a limestone boulder at Gislövshammar, Scania, Sweden, representing the upper part of the *A. atavus* Zone in the Alum Shale Formation.

Material and occurrence. – Only one pygidium was found in the *A. atavus* Zone at Fjällbränna.

The species is common in the upper part of the *A. atavus* Zone of Scania and the *A. atavus* and *P. punctuosus* zones of Bornholm (Weidner & Nielsen 2014), but it is rare in Norway (Høyberget & Bruton 2008). It is described as not rare within the upper part of the *A. atavus* Zone of Great Britain (Rushton 1979), and in eastern Newfoundland it is reported from the upper part of the *Mawddachites hicksii* Zone and the lower part of the *P. davidis* Zone (Hutchinson 1962), which corresponds to the upper part of the *A. atavus* and the *P. punctuosus* zones of Scandinavia.

Remarks. – The pygidium of '*D.*' *depressa* is about 10% wider than long. It is characterized by a wide border delimited by a wide border furrow that both widen considerably rearwards. The axis is approximately parallel-sided for ⅔ of its length, then tapers gently to a point and rarely reaches the border furrow; it may have a tiny secondary node at about the posteroaxis midlength (Fig. 36B) and the rear part of the posteroaxis is depressed. The axial node on M2 is elongate and stretches from F1 to F2 (Fig. 36B; Weidner & Nielsen 2014, fig. 30). Similarity is especially with smaller pygidia of '*D.*' *quadrata* that have a similar overall outline and likewise a depressed posterior part of the posteroaxis and a tiny secondary node. '*Diplorrhina*' *quadrata* differs, however, in having an axis that rapidly tapers straight to a sharp point. In the few published illustrations of '*D.*' *quadrata*, the axis never reaches the border furrow (Westergård 1946; Buchholz 2010).

The cephala of the two species also look quite similar. In '*D.*' *depressa*, the glabellar furrows F1 and F2 are indicated as constrictions and F3 is straight or bent a little backwards (Høyberget & Bruton 2008; Weidner & Nielsen 2014). In '*D.*' *quadrata*, the glabellar segmentation is more pronounced and F3 is distinctly bent backwards (Fig. 36J–K; see Tullberg 1880; Westergård 1946). In both species, the end lobe has a bulbous termination and the cephalic node is situated on the anterior part of M2. The basal lobes are simple and large.

Sloan & Laurie (2004) synonymized '*D.*' *depressa* with '*D.*' *quadrata*, but recently described material of '*D.*' *depressa* from Scania and Bornholm (Weidner & Nielsen 2014) clearly warrants a separation.

'*Diplorrhina*' *cylindrica* (Westergård, 1946) was not found in the study area but occurs in the *P. punctuosus* Zone of Scania and Bornholm. The pygidium of '*D.*' *cylindrica* is very similar to that of '*D.*' *depressa* and differs from the latter mainly in a rounded tip of the axis instead of tapering to a point. In '*D.*' *quadrata* the pygidium is wider than long and the axis tapers rapidly and straight to a pointed tip. The differences of ‘*D.*’ *cylindrica* to ‘*D.*’ *depressa* and ‘*D.*’ *quadrata* are observed in the cephalon and are distinct. The border of ‘*D.*’ *cylindrica* is anteriorly extremely wide and both border and border furrow taper out level F1, F3 is strongly bent backwards, and the posterior lobe ends indented by large basal lobes and is right angled instead of being bulbous as in ‘*D.*’ *depressa* and ‘*D.*’ *quadrata*. The cephalon of ‘*D.*’ *cylindrica* is more subquadrate in overall shape than the cephala of the other two species and it is widest in front of the glabella, while the greatest width in ‘*D.*’ *depressa* and ‘*D.*’ *quadrata* is at midlength of the anteroglabella.

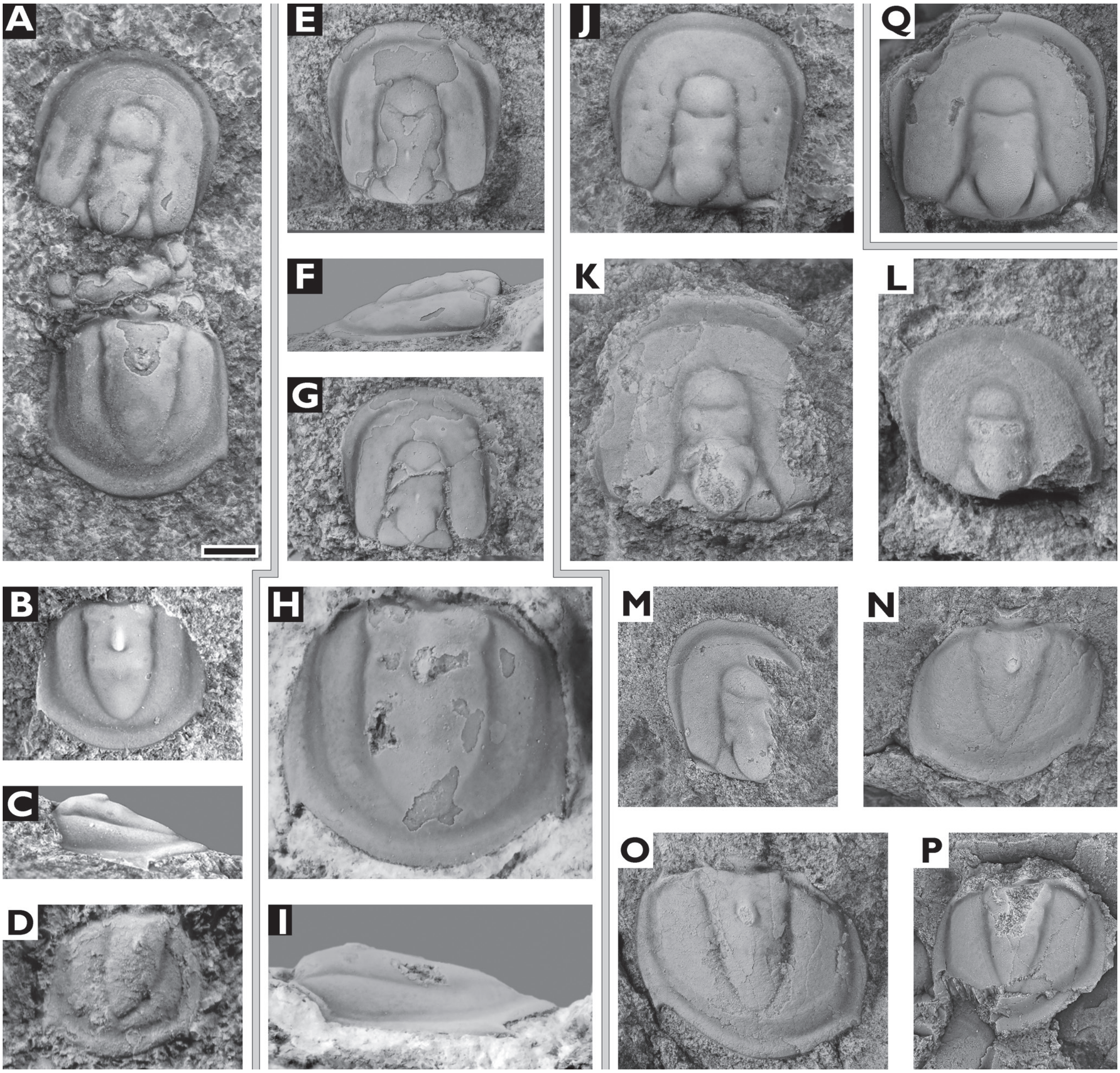


Fig. 36. A–D, ‘***Diplorrhina depressa***’ (**Westergård, 1946**). **A**, complete specimen from Gislövshammar, Scania, *A. atavus* Zone, for comparison with cephala and pygidia of *D. cylindrica* and *D. quadrata*. PMU 37183. **B**–**C**, pygidium in dorsal and lateral views. Note the depressed posteroaxis. From the *P. punctuosus* Zone at Øleå, Bornholm, Denmark. MGUH 30104. The specimen was illustrated by Weidner & Nielsen (2014, fig. 30J–K). **D**, pygidium from Fjällbränna. PMU 37182. ‘***Diplorrhina***’ ***cylindrica*** (**Westergård, 1946**). **E**–**F**, cephalon in dorsal and lateral views, and **G**, cephalon. Both are from the *P. punctuosus* Zone at Brantevik, Scania. PMU 38338 and 38339. **H**–**I**, **holotype** pygidium, SGU 4737, in dorsal and lateral views. From the *P. punctuosus* Zone at Gislövshammar, Scania. The specimen was illustrated by Westergård (1946, pl. 3, fig. 18). ‘***Diplorrhina***’ **quadrata** (**Tullberg, 1880**), all from the lower part of the *L. laevigata* Zone. **J**, cephalon with pitted surface and arcuate furrows from Brantevik, Scania. PMU 37185. **K**, cephalon, PMU 26202, from Karbäcken. **L**, cephalon, PMU 37184/1, from Fjällbränna. **M**, cephalon, PMU 26140/3, from Vedjeön. **N**–**P**, pygidia. PMU 26595, 26605/2, 26203. N and O are from Abborrfallet, P is from Karbäcken. ‘***Diplorrhina***’ **sp.**, **Q**, cephalon, from Stendalsbäcken, *P. punctuosus* Zone. PMU 23078/1. Scale bar = 1 mm.

'*Diplorrhina*' *quadrata* (Tullberg, 1880)

Figure 36J–P

1880 *Agnostus quadratus* n. sp. Tullberg, p. 34, pl. 2, fig. 25a, b.
1902 *Agnostus quadratus* Tullberg; Grönwall, p. 72.
1946 *Peronopsis quadrata* (Tullberg); Westergård, p. 40, pl. 3, figs 22–29.
1946 *Peronopsis quadrata sulcata* subsp. n. Westergård, p. 40, pl. 4, figs 1, 2.
1972 *Peronopsis quadrata* (Tullberg); Pokrovskaya & Egorova *in* Savitsky *et al.*, p. 63, pl. 6, figs 10, ?11.
1976 *Peronopsis quadrata* (Tullberg); Egorova *et al.*, p. 63, pl. 36, figs 1, 2, 4; pl. 37, figs 5, 6; pl. 38, figs 5, 22.
1994 *Quadragnostus quadratus* (Tullberg); Rudolph, p. 151, pl. 9, fig. 12.
1994 *Diplorrhina quadrata* (Tullberg); Robison, p. 38.
pars 1997 *Quadragnostus quadratus* (Tullberg); Buchholz, pp. 204, 243, pl. 19, figs 11, 12; *non* fig. 10 [= '*Diplorrhina*' *depressa* (Westergård, 1946)].
2002 *Quadragnostus quadratus* (Tullberg); Schöning, fig. 12.
2004 *Diplorrhina quadrata* (Tullberg); Sloan & Laurie, p. 198, fig. 2K.
2010 *Quadragnostus quadratus* (Tullberg); Buchholz, pl. 3, fig. 10.
2020 *Quadragnostus depressa*; Noriega-Ruiz *et al.*, fig. 9b [*non* 9a as stated in caption].

Lectotype (designated by Westergård 1946). – Pygidium, LO 400t, illustrated by Westergård (1946, pl. 3, fig. 22). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – One cephalon was found at Fjällbränna and a few specimens were collected at Vedjeön and Abborrfallet (northern Jämtland) and Karbäcken on the Tåsjö Mountain. They all originate from the lower part of the *L. laevigata* Zone. Elsewhere in Scandinavia, this rare species is known from the same zone in the Swedish provinces Scania and Västergötland (Westergård 1946) and from Bornholm, Denmark (Grönwall 1902). A few specimens have also been found in ice-rafted boulders in northern Germany deriving from the same stratigraphical level but also from the older *P. punctuosus* Zone (Rudolph 1994; Buchholz 1997, 2010). Outside Baltica, it has been reported from the early *L. laevigata* Zone in Australia (Sloan & Laurie 2004) and from the *P. praecurrens – T. gibbus* interval in Mexico (Noriega-Ruiz *et al.* 2020), which is an unusual early occurrence for this species.

Remarks. – For characteristic features of '*D.*' *quadrata* and its differentiation from '*D.*' *cylindrica* and '*D.*' *depressa*, see remarks on the latter. Cephala with scrobiculation and a weak furrow in the posterior part of the preglabellar field (Fig. 36J, K) were assigned to *Peronopsis* [here '*Diplorrhina*'] *quadrata sulcata* by Westergård (1946). Intraspecific variation of the exterior sculpture on the cheeks has been observed in many Scandinavian species, see remarks on *Onymagnostus hybridus*. Hence, we agree with Høyberget & Bruton (2008) to suppress *sulcata*.

'*Diplorrhina*' sp.

Figure 36Q

Material and occurrence. – One cephalon was found in the *P. punctuosus* Zone at Stendalsbäcken.

Description. – The cephalon is subquadrate in outline. The border and border furrow are wide anteriorly and narrow posteriorly. The cheeks are of even width throughout. The axial furrows and F3 are moderately wide and deep, the basal furrows are deep and narrow and F1 and F2 are effaced and only represented by faint constrictions. F3 is bent a little backwards. The end lobe is truncate. An occipital band connects the basal lobes which are unusual large compared to the other three species of '*Diplorrhina*'. The cephalic node is situated at the anterior edge of M2.

The described cephalon is distinguished from '*D.*' *depressa* and '*D.*' *quadrata* (both with a bulbous endlobe) and '*D.*' *cylindrica* (with a right-angled endlobe) in having an almost truncate endlobe. It further differs from these species by having barely visible constrictions at F1 and F2, a more anteriorly placed node and larger basal lobes. There is no similarity to cephala of '*Diplorrhina*' species occurring in the Czechia, Russia, Greenland or Australia.

Family Diplagnostidae Whitehouse, 1936

Genus *Acadagnostus* Kobayashi, 1939

Type species (OD). – *Agnostus acadicus* Hartt in Dawson, 1868, from the *Eccaparadoxides eteminicus* Zone, New Brunswick, Canada.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Robison (1994) considered *Acadagnostus* Kobayashi, 1939 as a possible synonym of *Peronopsis* Hawle & Corda, 1847. We prefer a more restricted interpretation of *Peronopsis*, and, hence, also of *Acadagnostus*; for details, see Weidner & Nielsen (2014, p. 59). In our interpretation six species from the Miaolingian of Scandinavia represent *Acadagnostus*, viz. *A. acadicus* (Hartt in Dawson, 1868), *A. scutalis* (Hicks, 1872) (*s.l.*), *A. minor* (Brøgger, 1878), *A. ferox* (Tullberg, 1880) and *A. brunfloensis* (Westergård, 1946).

Acadagnostus acadicus (Hartt *in* Dawson, 1868)

Figure 37A–P

pars 1868 *Agnostus acadicus*, sp. nov. Hartt *in* Dawson, p. 655, fig. 229 (cephalon only).
1869 *Agnostus fallax* n. sp. Linnarsson, p. 81, pl. 2, figs 54, 55.
1936 *Peronopsis fallax* (Linnarsson); Westergård, p. 28, pl. 1, figs 9–15.
1946 *Peronopsis fallax* (Linnarsson); Westergård, p. 37, pl. 2, figs 18–24.
1990 *Axagnostus fallax* (Linnarsson); Laurie, p. 319, fig. 1 A–D, F, H–J.
1995 *Peronopsis acadica* Hartt (in Dawson); Robison, p. 302 (*cum syn*., we have not checked all), fig. 1:1–3.
1997 *Acadagnostus fallax* (Linnarsson); Shergold & Laurie, p. 362, fig. 230:8a, b.
2008 *Peronopsis fallax* (Linnarsson); Høyberget & Bruton, p. 28, pl. 3, figs A–H.
2009b *Peronopsis acadica* Hartt (in Dawson); Peng *et al*., p. 19, figs 12:1–12 & 15:12–13.
2014 *Acadagnostus acadicus* Hartt; Danukalova, Kuzmichev & Korovnikov, pl. 2, fig. 6.
2014 *Acadagnostus acadicus* Hartt (*in* Dawson); Weidner & Nielsen, p. 60, fig. 32A–C.
2014 *Acadagnostus acadicus* Hartt (*in* Dawson); Weidner *et al*., p. 529 (*cum syn*.), fig. 16C–F.

Holotype (by monotypy, see Robison 1995). – Cephalon, GSC 30178, illustrated by Hartt (*in* Dawson 1868, fig. 229), re-illustrated by Robison (1995, fig. 1:1). It derives from the *A. atavus* Zone, Forest Hills Formation at St. John, New Brunswick, Canada.

Material and occurrence. – About 20 cephala and pygidia were found in the lower part of the *A. atavus* Zone at Fjällbränna and Djupdalsbäcken. On the Tåsjö Mountain, a few more specimens were found at Högnäsån and Bellviks Hällan, and abundant material was collected at Tåsjö church from the same zone. Kulling (1955) noted occurrence at Långseleån, Skansholm and Lubbträsk in the *T. gibbus* Zone. The species is rare in the *A. pinus – P. praecurrens* Zone at Marbäcken and Rökbergsbäcken (Kulling 1955; Weidner *et al*. 2014). Overall, *A. acadicus* appears to be rare in Västerbotten. The species is otherwise known from all Swedish provinces (Westergård 1946) as well as from Norway (Strand 1929; Høyberget & Bruton 2008) and Bornholm, Denmark (Weidner & Nielsen 2014). It is a cosmopolitan species (usually reported as *P. fallax*) that occurs in many countries (Robison 1995). It ranges from the *A. pinus – P. praecurrens* Zone through the *P. punctuosus* Zone and shows especially in the pygidium considerable variations (see Laurie 1990).

Remarks. – As currently defined, *A. acadicus* is a quite variable and long-ranging species, and it is possible that it covers more than one species (cf. Laurie 1990). Pending a revision, we adopt the 'broad' interpretation of this form. Høyberget & Bruton (2008, p. 29) considered *A. acadicus* to be a *nomen dubium*.

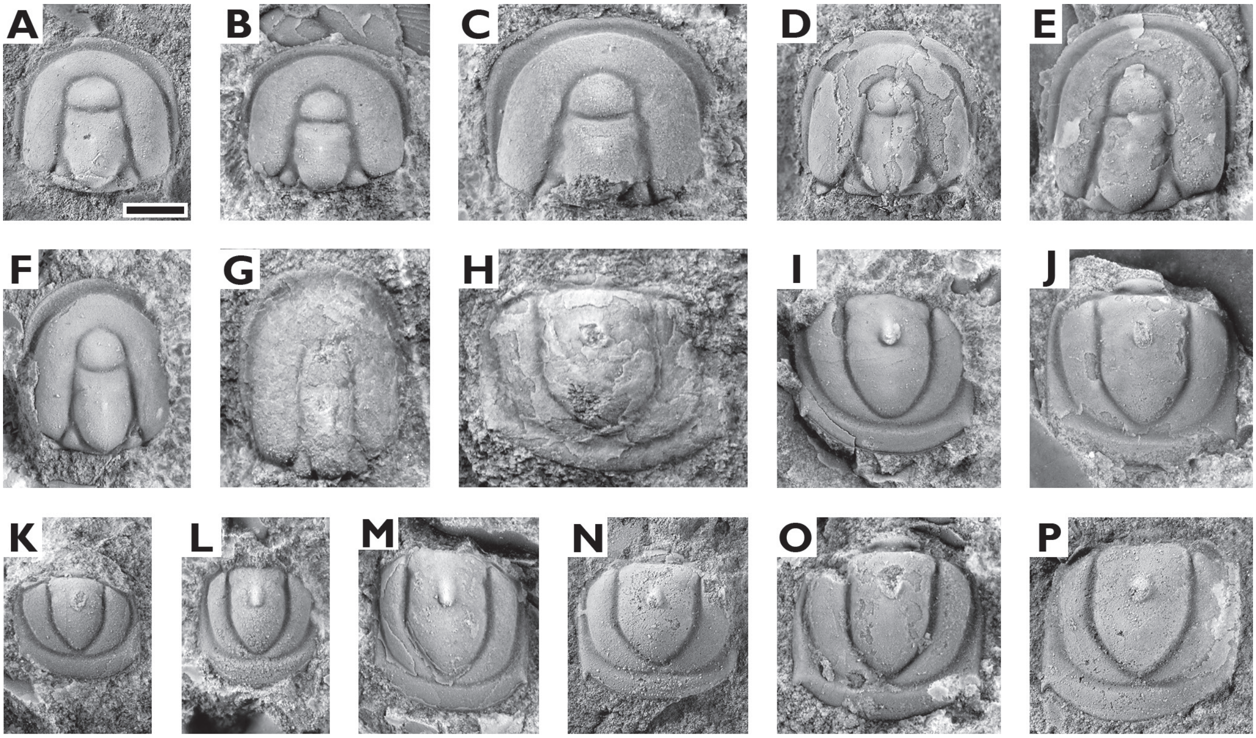


Fig. 37. ***Acadagnostus acadicus* (Hartt in Dawson, 1868)**, *A. atavus* Zone. **A–G**, cephala. PMU 26177a/2, 37187/2, 37187/1, 26175, 37188/1, 37186, 37190/1. **H–P**, pygidia. PMU 37190/2, 37191, 37188/3, 37188/2, 37192/1, 37193/1, 26177a/1, 37189, 26177a/3. A, N and P are from Tåsjö church. B–C, E–F, I–M and O are from Djupdalsbäcken. D is from Bellviks Hällan and G–H are from Fjällbränna. Scale bar = 1 mm.

Acadagnostus ferox (Tullberg, 1880)

Figure 38A–V

1878 *Agnostus fallax*, Linnarsson var. 4 Brøgger, p. 64, pl. 6, fig. 1.
1880 *Agnostus fallax* Linnarsson, forma ferox Tullberg, p. 31, fig. 23.
1946 *Peronopsis fallax ferox* (Tullberg); Westergård, p. 38, pl. 2, fig. 27a, b; pl. 3, figs 1, 2.
pars 1991 *Peronopsis fallax ferox* (Tullberg); Yang *et al*., p. 108, pl. 1, fig. 22; pl. 2, figs 16–18; pl. 3, fig. 2; *non* fig. 1 [= *Acadagnostus acadicus* (Hartt *in* Dawson, 1868)].
1994 *Peronopsis ferox* (Tullberg); Robison, p. 44, fig. 19. 1, 2.
2008 *Peronopsis ferox* (Tullberg); Høyberget & Bruton, p. 29, pl. 3, figs I–P.
2010 *Peronopsis fallax ferox* (Tullberg); Buchholz, pl. 3, figs 11, 12.
2014 *Acadagnostus ferox* (Tullberg); Weidner & Nielsen, p. 61 (*cum syn.*), fig. 32D.

Lectotype (designated by Westergård 1946). – Pygidium, LO 396t, originally illustrated by Tullberg (1880, pl. 2, fig. 23b) and refigured by Westergård (1946, pl. 2, fig. 27). It derives from the *P. punctuosus* Zone of the Alum Shale Formation at Borggård, Øleå, Bornholm, Denmark.

Material and occurrence. – Acadagnostus ferox occurs at Abborrfallet and Strömnäs in the *P. punctuosus* and *G. nathorsti* zones, at Granberget in the *P. punctuosus* Zone, and at Långseleån, Fjällbränna, Skansholm, Stalon and Sågbäcken in the *G. nathorsti* Zone. Karbäcken on the Tåsjö Mountain is the only locality where it may range into the lower part of the *L. laevigata* Zone. In Sweden and Norway, the species is reported from many Cambrian provinces and ranges from the *P. punctuosus* Zone into the lower part of the *L. laevigata* Zone, but in Norway rare specimens appear in the *A. atavus* Zone (Westergård 1946; Bruton & Harper 2000; Høyberget & Bruton 2008). On Bornholm, Denmark, it is recorded from the *A. atavus* Zone to the lower part of the *L. laevigata* Zone (Grönwall 1902; Weidner & Nielsen 2014). It has also been reported from strata corresponding to the *A. atavus* Zone in Utah, USA (Robison 1972a), Australia (Öpik 1979) and Greenland (Robison 1994).

Remarks. – Acadagnostus ferox was described in detail by Høyberget & Bruton (2008). These authors also remarked on differences from the similar *A. acadicus* (treated as *Peronopsis fallax*) and a large number of specimens were illustrated of both species. All pygidia from the Lower Allochthon have the characteristic confluent pleural fields which distinguish the species from *A. acadicus*, in which the axis either reaches the border furrow or where a short postaxial furrow separates the pleural fields.

Acadagnostus minor (Brøgger, 1878)

Figure 39A–P

1878 *Agnostus fallax* Linnarsson, var. 3 Brøgger, p. 65.
1929 *Agnostus fallax* Linnarsson; Strand, p. 346.
pars 1946 *Peronopsis fallax minor* (Brögger); Westergård, p. 38, pl. 3, figs 3, 6; *non* figs 4, 5, 7 [= indet.].
1966 *Peronopsis fallax minor* (Brögger); Sdzuy, p. 65, pl. 8, figs 1–5.
non 1978 *Peronopsis fallax* (Linnarsson) *minor* (Brögger); Rushton, p. 251, pl. 24, fig. 1 [= indet.].
1982 *Peronopsis minor* (Brögger); Robison, p. 153.
1990 *Peronopsis fallax minor* (Brögger); Laurie, p. 322.
non 1991 *Peronopsis fallax minor* (Brögger); Yang *et al*., p. 108, pl. 2, figs 10–14 [= indet.].
2000 *Peronopsis minor* (Brøgger); Bruton & Harper, p. 33.
non 2008 *Peronopsis minor* (Brögger); Ergaliev & Ergaliev, p. 147, pl. 8, fig. 19 [= indet.].
2008 *Peronopsis minor* (Brøgger); Høyberget & Bruton, p. 32, pl. 3, figs R–W.
non 2010 *Peronopsis fallax minor* (Brögger); Buchholz, pl. 2, figs 4, 5 [= indet.].

Lectotype (designated by Høyberget & Bruton 2008). – Pygidium, PMO 28903, from the Brøgger collection and figured by Høyberget & Bruton (2008, pl. 3, fig. V). The specimen is from the lower part of the *L. laevigata* Zone at Krekling, Oslo Region, Norway. It is re-illustrated here in Fig. 39E.

Paralectotype. – Cephalon, PMO 28904, from the same locality and zone, figured by Høyberget & Bruton (2008, pl. 3, fig. R), and here re-illustrated in Figure 39A. This cephalon is preserved flattened in shale and has a wide border furrow but other cephala from Norway show the diagnostic narrow border furrow.

Material and occurrence. – Acadagnostus minor was reported from the lower part of the *L. laevigata* Zone at Vedjeön and Abborrfallet by Westergård (1946). We have not found any new material. In southern Norway, it occurs at the same stratigraphical level (Brøgger 1878; Høyberget & Bruton 2008). Westergård (1946) reported the species also from Scania, but without illustrations. As two of the four specimens he figured from Abborrfallet do not represent *A. minor*, this occurrence seems doubtful.

Remarks. – Westergård (1946) described the species based on specimens from Abborrfallet (northern Jämtland) but he illustrated two distinctly different cephala and two distinctly different types of pygidia (Laurie 1990). Høyberget & Bruton (2008) published the first diagnosis and gave a detailed description of *A. minor* based on one pygidium from Brøgger`s collection and some newly collected cephala and pygidia from Norway. Only one cephalon and one pygidium

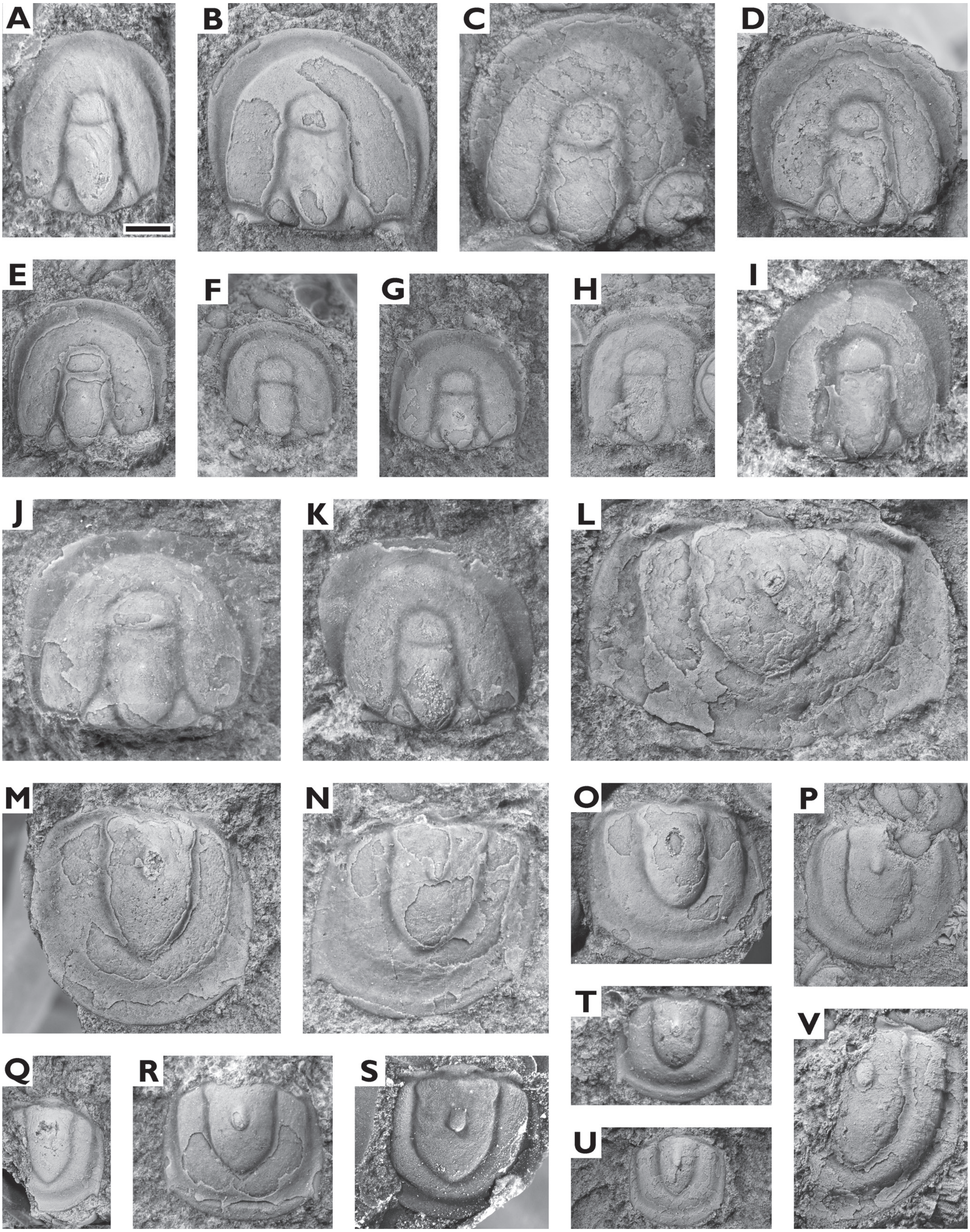


Fig. 38. ***Acadagnostus ferox*** (**Tullberg, 1880**). **A**–**K**, cephala. PMU 37180/2, 23048, 23050/1, 23053, 23055, 23063/4, 23059, 23063/3, 37195, 37196, 37198/1. **L**–**V**, pygidia. PMU 23051, 23052, 37194, 23056, 23063/1, 23062/3, 37197/1, 23049, 37197/2, 23058, 23057. A–B and S, from the *P. punctuosus* Zone at Granberget. C–E and L–M, O, from the *G. nathorsti* Zone at Fjällbränna. F, H, N and P–Q, from the *G. nathorsti* Zone at Långseleån. G, I–K and R, T–U, from the *G. nathorsti* Zone at Skansholm. V, from the *G. nathorsti* Zone at Stalon. Scale bar = 1 mm.

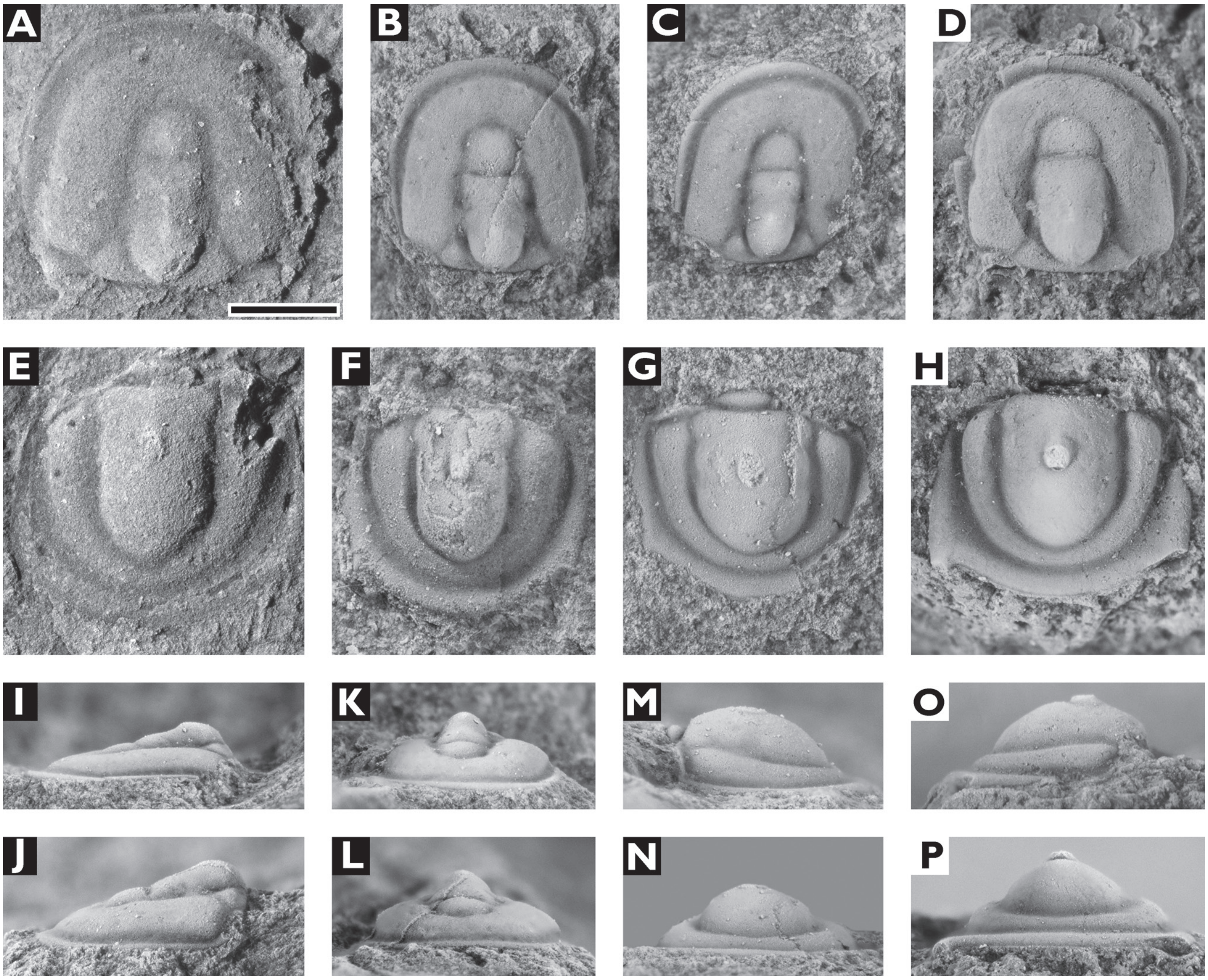


Fig. 39. ***Acadagnostus minor*** (**Brøgger, 1878**), *L. laevigata* Zone. **A**–**D**, **I**–**L**, cephala. **A**, paralectotype cephalon flattened in shale, from Krekling, Norway, PMO 28904. B, J, L in dorsal, lateral and anterior views, Gjøvik, Norway, PMO 211949. C, I, K in dorsal, lateral and anterior views, Gjøvik, Norway, PMO 211948. D is from Abborrfallet, SGU 4725. **E**–**H**, **M**–**P**, pygidia. E, **lectotype** pygidium flattened in shale, from Krekling, Norway, PMO 28903. F is from Gjøvik, Norway, PMO 211951. G, M, N in dorsal, lateral and posterior views, Gjøvik, Norway, PMO 211950. H, O, P in dorsal, lateral and posterior views, Abborrfallet, SGU 4728. All specimens from Norway were illustrated by Høyberget & Bruton (2008, pl. 3, figs R–W) and the two specimens from Sweden by Westergård (1946, pl. 3, figs 3 & 6). Scale bar = 1 mm. Note that the magnification is larger than used for most agnostoid illustrations in this publication.

illustrated by Westergård (1946) were considered by them to belong to *A. minor* and we agree with that assessment. The key feature of the cephalon is the narrow border furrow which distinguishes *A. minor* from *A. fallax* and *A. ferox* both of which possess a wide border furrow (Figs 37, 38). Characteristic for the pygidium is a long and broad axis with a rounded posterior tip and confluent pleural fields of approximately the same width throughout. *Acadagnostus ferox* has confluent pleural fields as well, but in both *A. fallax* and *A. ferox* the axis is proportionally narrower and has a pointed termination (Figs 37, 38). The species is small and attains rarely a length of more than 2 mm. Illustrations in Høyberget & Bruton (2008, pl. 3) allow a clear differentiation of the three species.

Peronopsis cf. *P. fallax minor* (Brögger, 1878) [*Peronopsis fallax minor* (Brögger, 1878) *sensu* Sdzuy 1966)] is reported by Geyer *et al.* (2019) from the Bergleshof-Schichten in the Frankenwald of Germany. The fauna has Scandinavian affinities and represents the lower part of the *L. laevigata* Zone (Sdzuy 1966; Geyer 2010; Geyer *et al.* 2019). The material complies well with that from Norway.

All other reports of *A. minor* from England, China, Kazakhstan and ice-rafted boulders from northern Germany (Rushton 1978; Yang *et al.* 1991; Ergaliev & Ergaliev 2008; Buchholz 2010) are sparsely illustrated and none of the specimens fall within the narrow definition of the species suggested by Høyberget & Bruton (2008). The figured material differs from

A. minor in having a wide cephalic border furrow and the pygidial axis reaches the border furrow, features reminiscent of *A. fallax*. Fortey & Rushton (1976, p. 326, pl. 12, figs 1–14) illustrated 14 cephala and pygidia of *Peronopsis fallax* (Linnarsson) aff. *minor* (Brögger) from middle Cambrian strata in Iran. Some of the pygidia (Fortey & Rushton 1976 figs 5 and 7), differ only insignificantly from the Norwegian and Swedish material figured herein by having a narrower postaxial field, and, if figured alone, would have been accepted as *A. minor*, while the specimen illustrated in figure 6 has an axis that reaches the border furrow. All associated cephala differ from the Scandinavian material in having either a wide border furrow, a pointed anteroglabella, a laterally expanded posteroaxis or larger basal lobes. Hence, it is possible that the Iranian specimens represent *A. minor* but more extensive Scandinavian material is needed to clarify intraspecific variation. For illustration of variability of cephalic features, see *H. pater* (Fig. 14).

Genus *Diplagnostus* Jaekel, 1909

Type species (OD). – *Agnostus planicauda* Angelin, 1851, from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Diagnosis. – See Shergold & Laurie (1997) and Peng & Robison (2000).

Remarks. – We discern three subspecies of *Diplagnostus* in the Miaolingian of Scandinavia: *Diplagnostus planicauda planicauda* (Angelin, 1851), *D. planicauda vestgothicus* (Wallerius, 1895) and *D. planicauda bilobatus* Kobayashi, 1939. These subspecies occur at different stratigraphical levels and mostly at different localities. Robison (1994) and Høyberget & Bruton (2008) treated these subspecies as one taxon.

Diplagnostus planicauda bilobatus Kobayashi, 1939

Figure 40A–U

1946 *Diplagnostus planicauda bilobatus* Kobayashi; Westergård, p. 62, pl. 8, figs 13–21.
1962 *Diplagnostus planicauda* (Angelin) forma *D. bilobatus* Kobayashi; Hutchinson, p. 78, pl. 7, figs 10–13.
?1975 *Diplagnostus planicauda* var. *bilobatus* Kobayashi; Repina, p. 103, pl. 9, fig. 1.
1982 *Diplagnostus planicauda bilobatus* Kobayashi; Egorova *et al.*, p. 61, pl. 11, fig. 8; pl. 34, fig. 18; pl. 46, fig. 1.
1991 *Diplagnostus planicauda bilobatus* Kobayashi; Dong, pl. 2, figs 4, 5.
1994 *Diplagnostus planicauda bilobatus* Kobayashi; Rudolph, p. 143, pl. 9, figs 14–17.
pars 2000 *Diplagnostus planicauda* (Angelin); Peng & Robison, p. 49, fig. 35:2, ?3, 4–6.
?2008 *Diplagnostus planicauda bilobatus* Kobayashi; Ergaliev & Ergaliev, pl. 22, fig. 18.
pars 2008 *Diplagnostus planicauda* (Angelin); Høyberget & Bruton, p. 23, pl. 1, R–S, V–W; pl. 2, figs A–B.
2014 *Diplagnostus planicauda bilobatus* Kobayashi; Weidner & Nielsen, p. 58 (*cum syn.*), fig. 31.

Neotype (designated by Westergård 1946). – Tullberg's original material of '*Agnostus*' *planicauda* seems to be lost, so Westergård (1946, pl. 8, fig. 16) proposed as neotype the cephalon, SGU 4863. It derives from the *G. nathorsti* Zone in the Alum Shale Formation at Kiviks-Esperöd, Scania, Sweden.

Material and occurrence. – *Diplagnostus planicauda bilobatus* occurs sparsely in the upper part of the *A. atavus* Zone at Abborrfallet, Fjällbränna, Dantas Mountain and Strömnäs whereas it is a dominant species in the *G. nathorsti* Zone at Fjällbränna, Skansholm, Strömnäs and Stalon. At several localities in northern Jämtland and on the Tåsjö Mountain, the subspecies is common also in the *P. punctuosus* Zone and the *P. forchhammeri* Superzone according to Westergård (1946). Elsewhere, the subspecies has been reported from the upper part of the *A. atavus* Zone and the *P. punctuosus* Zone of Bornholm (Grönwall 1902; Weidner & Nielsen 2014), the *G. nathorsti* Zone of Norway (Høyberget & Bruton 2008) and from the *P. punctuosus* and *G. nathorsti* zones in the Swedish provinces Scania and Västergötland (Westergård 1946). In the latter area it also ranges into the basal *L. laevigata* Zone at Munkesten, Hunneberg. *Diplagnostus planicauda bilobatus* is further known from the *P. punctuosus* Zone of North Greenland (V. Poulsen 1969), the *P. davidis* Zone and the *P. forchhammeri* Superzone of eastern Newfoundland (Hutchinson 1962) and from corresponding strata (*Anopolenus henrici* Zone) in Siberia (Egorova *et al.* 1982). *Diplagnostus planicauda bilobatus* occurs also in S. China (Peng & Robison 2000).

Remarks. – *Diplagnostus planicauda bilobatus, D. planicauda planicauda* and *D. planicauda vestgothicus*, which in Scandinavia occur at different stratigraphical levels although with some overlap, are closely allied. For detailed remarks on distinguishing characters, see Weidner & Nielsen (2014, p. 59); we here maintain a distinction as chronosubspecies, but emphasize that not all authors agree in this approach.

The new material from the Lower Allochthon is assigned to the subspecies *bilobatus*, as none of the

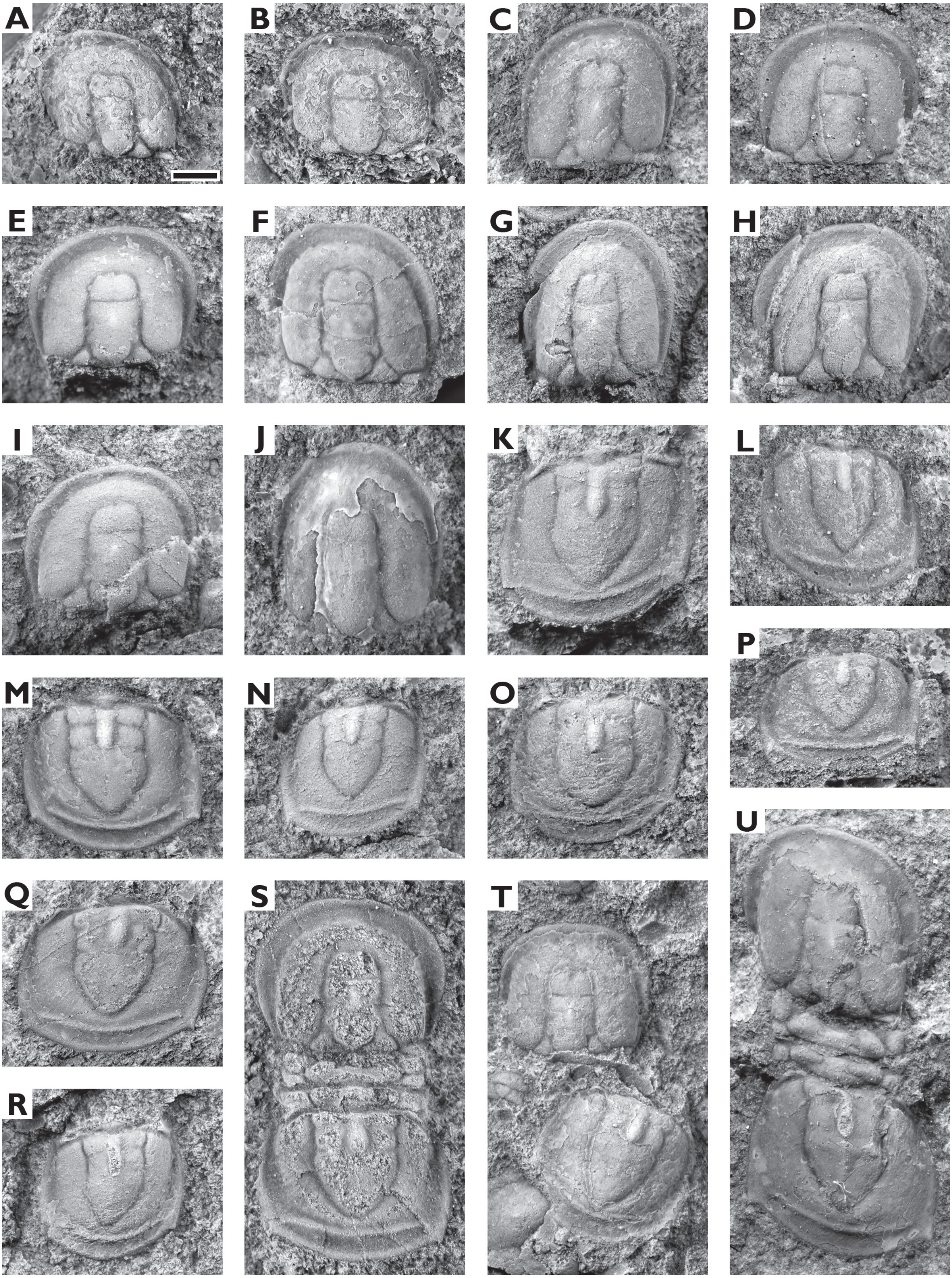


Fig. 40. ***Diplagnostus planicauda bilobatus*** **Kobayashi**, **1939**, *G. nathorsti* Zone. **A**–**J**, cephala. PMU 37199, 37200, 37208/2, 37206/1, 37208/1, 37204, 37208/3–37208/5, 37208/7. **K**–**R**, pygidia. PMU 37205, 37206/2, 37208/6, 37208/8, 37208/9, 37209, 37212, 37208/10. **S**–**U**, complete specimens. PMU 37203, 37091/2, 37207. A–T are from Fjällbränna, U is from Skansholm. Scale bar = 1 mm.

cephala show a median preglabellar furrow and all pygidia are widest at M1, two features characteristic for this subspecies (Weidner & Nielsen 2014).

Genus *Linguagnostus* Kobayashi, 1939

Type species (OD). – *Agnostus kjerulfi* Brøgger, 1878, from the *Paradoxides forchhammeri* beds in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – Two species, *L. kjerulfi* (Brøgger, 1878) and *L. groenwalli* Kobayashi, 1939, are known from the Miaolingian of Scandinavia.

Linguagnostus kjerulfi (Brøgger, 1878)

Figure 41A–C, E–G and I–K

1878 *Agnostus kjerulfi* n. sp. Brøgger, p. 65, pl. 5, fig. 7.

1880 *Agnostus kjerulfi* Brögger; Tullberg, p. 32.

non 1902 *Agnostus kjerulfi* Brögger; Grönwall, p. 69, pl. 1, fig. 11 [= *L. groenwalli* Kobayashi, 1939].

non 1916 *Agnostus kjerulfi* Brögger; Nicholas, p. 459, pl. 39, fig. 3 [= indet.].

non 1916 *Agnostus kjerulfi* Brögger; Illing, p. 417, pl. 32, fig. 6 [= *L. groenwalli* Kobayashi, 1939].

1930 *Agnostus kjerulfi* Brögger; Westergård *in* Holm & Westergård, pl. 4, figs 13, 14.

1939 *Linguagnostus kjerulfi* (Brögger); Kobayashi, p. 142 [*Linguagnostus* erected].

1946 *Linguagnostus kjerulfi* (Brögger); Westergård, p. 64, pl. 8, figs 31, 32; pl. 9, figs 1–3.

1989 *Linguagnostus transversus* (sp. nov.) Lu & Lin, p. 77, 203, pl. 3, fig. 9.

1990 *Linguagnostus kjerulfi* (Brögger); Shergold, Laurie & Sun, p. 82, fig. 14:6a, b.

1991 *Linguagnostus kjerulfi* (Brögger); Yang *et al*., p. 117, pl. 7, figs 1–3.

1997 *Linguagnostus kjerulfi* (Brögger); Shergold & Laurie, p. 364, fig. 230:5a, b.

pars 1999 *Linguagnostus kjerulfi* (Brøgger); Bruton, p. 340, fig. 3A, B; *non* fig. 3C, D [= *Acadagnostus ferox* (Tullberg, 1880)].

2000 *Linguagnostus kjerulfi* (Brøgger); Peng & Robison, p. 52 (*cum syn.*), fig. 38.

2008 *Linguagnostus kjerulfi* (Brögger); Ergaliev & Ergaliev, p. 160, pl. 13, fig. 17.

2008 *Linguagnostus kjerulfi* (Brøgger); Høyberget & Bruton, p. 24. pl. 2, figs C–K.

2009b *Linguagnostus kjerulfi* (Brøgger); Peng *et al*., p. 11.

Lectotype (designated by Westergård 1946). – Pygidium, PMO 28684, originally figured by Holm & Westergård (1930, pl. 4, fig. 14), refigured by Westergård (1946, pl. 8, fig. 32), Shergold & Laurie (1997, fig. 230:5b) and Bruton (1999, fig. 3B). The specimen is from the *P. forchhammeri* Superzone in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Paralectotype. – Cephalon, PMO 28682, same level and locality as the lectotype. Originally figured by Westergård in Holm & Westergård (1930, pl. 4, fig. 13), refigured by Westergård (1946, pl. 8, fig. 31), Shergold & Laurie (1997, fig. 230:5a) and Bruton (1999, fig. 3A).

Material and occurrence. – Three cephala and six pygidia, mostly fragmentary, were collected from one small limestone concretion at Fjällbränna; one additional pygidium was found at Långseleån. Other material is from Högnäsån on the Tåsjö Mountain (two pygidia) and from Vedjeön in northern Jämtland (two cephala). The species was reported from Fånån by Asklund & Thorslund (1935). Elsewhere, *L. kjerulfi* is described from Scania (Westergård 1946), the Oslo Region, Norway (Høyberget & Bruton 2008), Kazakhstan (Ergaliev & Ergaliev 2008), Indian Himalaya (Peng *et al*. 2009b) and China (Peng & Robison 2000). Everywhere it occurs in the lower part of the *L. laevigata* Zone; only in China is seen a range into the basal upper part of this zone.

Discussion. – *Linguagnostus kjerulfi* is very characteristic and well-preserved cephala are readily differentiated from contemporaneous agnostoids, of which only *D. planicauda bilobatus* and *A. ferox* show some cephalic resemblance, while the pygidium is unique. The cephalon of *L. kjerulfi* is characterized by an exceptionally broad anterior border furrow, an anteroglabella with a short frontal sulcus, an angular or rounded posterior tip of the posteroglabella, large basal lobes and cheeks that laterally often are twice as wide as anteriorly (Fig. 41A–C, E; Høyberget & Bruton 2008, pl. 2, figs C–F). The pygidium has a pair of lateral spines and one mesial spine. A sinuous ridge separates the pleural fields posteriorly and laterally from the broad border furrow and runs back to the base of the lateral spines. For a more exhaustive description of the species, see Peng & Robison (2000) and Høyberget & Bruton (2008). The illustrated cephala from China (Peng & Robison 2000) all have a posteroglabella with an angular end, narrower cephalic border furrows and the cheeks are narrowing less forwards than in the Scandinavian material.

Linguagnostus groenwalli Kobayashi, 1939 occurs in the *P. punctuosus* Zone of Scandinavia (Weidner & Nielsen 2007). The only observable difference in the cephalon between *L. kjerulfi* and *L. groenwalli* is the presence of an anteroglabellar cleft in the former and which is not seen in the latter (Westergård 1946, pl. 8, fig. 31 versus Fig. 41D and Weidner & Nielsen 2007, fig. 2A). However, only one cephalon

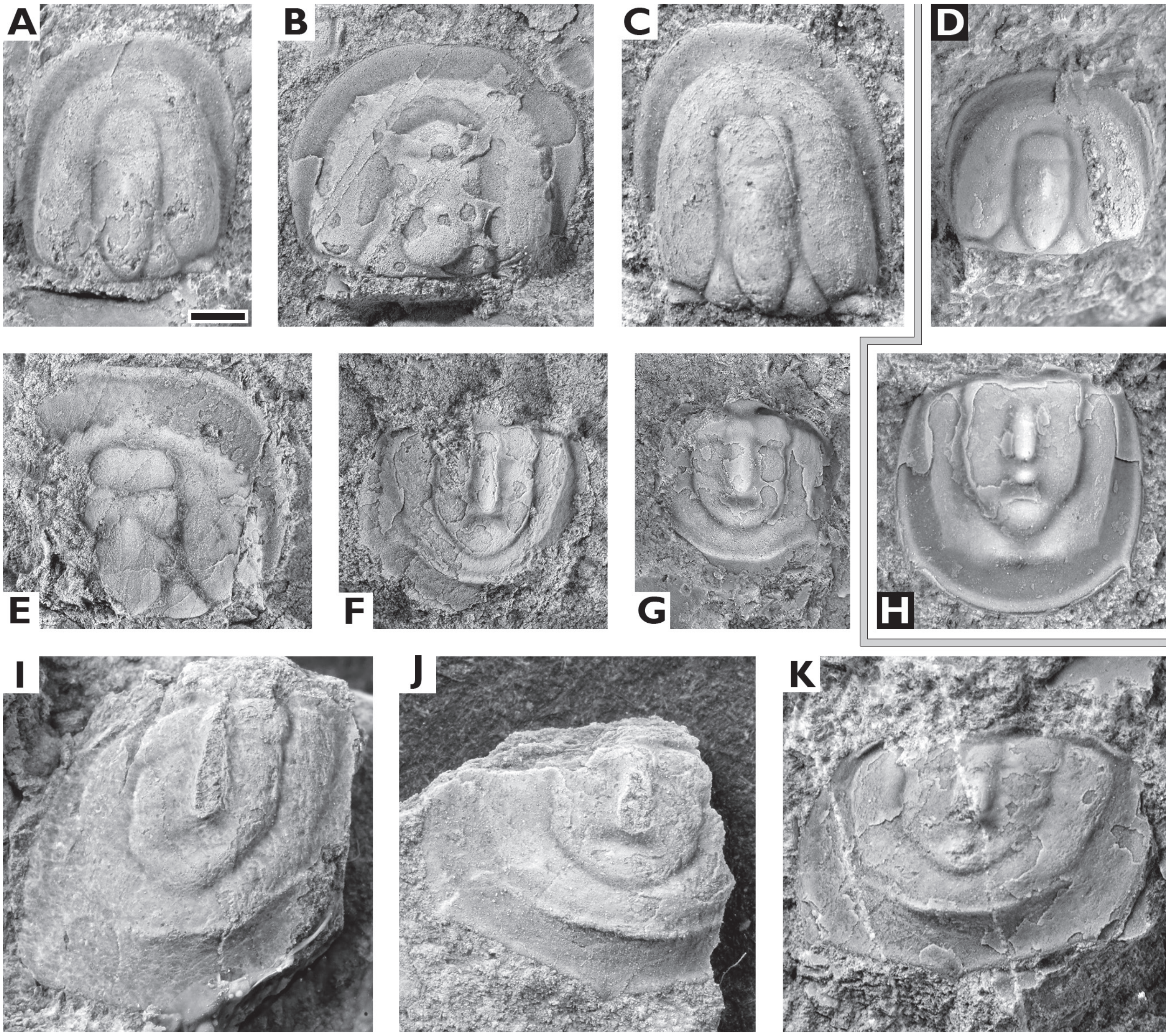


Fig. 41. ***Linguagnostus kjerulfi*** **(Brøgger, 1878)**, lower part of the *L. laevigata* Zone. **A–C**, **E**, cephala. PMU 36427/2, 26143/1, 37214/1, 26141/2. **F–G** and **I–K**, pygidia. PMU 26246/1, 26247, 37215, 37216, 37213. A, C, I and K are from Fjällbränna. B and E are from Vedjeön. F and G are from Högnäsån and J is from Långseleån. ***Linguagnostus groenwalli*** **Kobayashi, 1939. D,** cephalon, MGUH 28387, and **H,** pygidium, MGHU 28388, shown for comparison. They originate from ice-rafted boulders of the *P. punctuosus* Zone, found at Ålehoved, Fyn, Denmark and have previously been illustrated by Weidner & Nielsen (2007, fig. 2A, B). Scale bar = 1 mm.

of *L. groenwalli* is illustrated from Scandinavia and cephala from Greenland and Siberia display such a cleft, and apparently this variable feature cannot be used to safely separate cephala of the two species (Pokrovskaya *in* Tchernysheva 1960, pl. 1, fig. 5; Robison 1994, fig. 10:1–2), but their pygidia differ. In *L. kjerulfi* the axis has a broad and elongate node, extending from the front of M1 to the transverse sulcus on M3 (Westergård 1946, pl. 8, fig. 32 [lectotype]); Peng & Robison 2000, fig. 38:4, 8). In *L. groenwalli*, the node extends from the rear of M1 to F2, and is here interrupted but continues on the posteroaxis as a stout knob just in front of the transverse sulcus (Fig. 41H; Egorova *et al*. 1982, pl. 14, fig. 6; Weidner & Nielsen 2007, figs 1 [lectotype], 2B–F). Further, in *L. groenwalli* the margin of the pygidium has no middle spine, M1 and M2 are poorly outlined and the posterior ridge is not connected with the posterolateral border. In larger holaspids the posterior border is zonate.

The newly collected cephala assigned to *L. kjerulfi* have an anteroglabellar cleft in the cephalon like the lectotype and anteriorly narrowing cheeks. The pygidium has an axial node of the same shape, a posterior axial ridge and two lateral and one posterior marginal spines.

Agnostus kjerulfi from the *P. punctuosus* Zone of the Abbey Shales of England (Illing 1916, pl. 32, fig. 6; refigured in Rushton 1979, fig. 8G) was rejected from the species by Westergård (1946), Rushton (1979) and Peng & Robison (2000), but they noted some resemblance to *L. groenwalli*. Newer illustrations of large holaspid pygidia published by Egorova *et al.* (1982, pl. 14, fig. 6) and Weidner & Nielsen (2007, fig. 2F) clearly identify this specimen as belonging to *L. groenwalli*.

Cephala of *D. planicauda bilobatus* have a narrower border furrow, a rounded posterior tip of the posteroglabella and cheeks of even width throughout (Fig. 40).

Cephala of *Acadagnostus ferox* can have a wide border furrow as in *L. kjerulfi* (Høyberget & Bruton 2008), but lack the frontal sulcus in the anteroglabella and have cheeks of even width throughout.

Family Phalacromidae Hawle & Corda, 1847

Genus *Lisogoragnostus* Rozova *in* Lisogor, Rozov & Rozova, 1988

Type species (OD). – *Lisogoragnostus kalisae* Rozova *in* Lisogor *et al.*, 1988, from the *Tomagnostus fissus* Zone, Amgan Stage, of southern Kazakhstan.

Diagnosis. – See Shergold & Laurie (1997) and Peng & Robison (2000).

Remarks. – *Lisogoragnostus* is known from Kazakhstan and Russia (*L. kalisae* Rozova, 1988), China (*Abagnostus circularis* Yang & Liu, 1991; *L. hybus* Peng & Robison, 2000; *L. mictus* Peng & Robison, 2000), South Korea (*L. coreanicus* Hong *et al.*, 2003; *L. minor* Kobayashi, 1962), Australia ('*Peratagnostus*' *nobilis* [*pars* Shergold 1982, pl. 6, figs 4–7]), northwestern Canada (*Phalagnostus shergoldi* Pratt, 1992), as well as Norway and Sweden including ice-rafted boulders in northern Germany (*L. confluentus*). Very sparse material is described also from Tasmania and northwestern Canada but these ocurrences cannot be safely assigned to species (Jago 1976; Pratt 1992). Both the cephalon and the pygidium, either as complete specimens or as detached skeletal parts in sufficient numbers, are required to safely identify species, as cephalic features vary highly between species, whereas pygidial characteristics especially in less well-preserved material may be difficult to recognize. Species are differentiated notably by the presence or absence of a cephalic border and border furrow and the variable development of cephalic furrows; in the pygidium the axial nodes show variable development between species.

Lisogoragnostus confluentus (Rudolph, 1994), which is the only representative known from Scandinavia, has a well-defined cephalic border and border furrow and furrows all around the posteroglabella and the basal lobes are distinct. The pygidial axis carries an elongate node as well as a terminal node. These characters are shared with *L. hybus* Peng & Robison, 2000, which we consider as a junior synonym (see below). *Lisogoragnostus kalisae* and *L. circularis* (Yang *et al.* 1991) possess a border furrow as well, but the cephalic furrows are partially or completely effaced and the basal lobes are vestigial. The pygidium of *L. kalisae* differs in the anteriorly situated and rounded axial node while *L. circularis* shows no obvious pygidial differences. All remaining species of *Lisogoragnostus*, *L. mictus* Peng & Robison, 2000, *L. minor* (Kobayashi, 1962), *L. coreanicus* Hong *et al.*, 2003, *L. shergoldi* (Pratt, 1992) and '*Peratagnostus*' *nobilis* Öpik, 1967 [*partim*], have cephala with partially or completely effaced border furrows. *Lisogoragnostus* ranges from the *A. atavus* Zone (Kazakhstan) to the early Furongian (Australia, Canada, USA).

Lisogoragnostus confluentus (Rudolph, 1994)

Figure 42A–X

1946 *Phalacroma* sp. Westergård, p. 97, pl. 16, fig. 3.
1967 *Hypagnostus parvifrons* (Linnarsson); Rasetti, p. 34, pl. 9, figs 23–25.
1967 Agnostida, pygidium no. 1; Rasetti, p. 38, pl. 10, figs 22–26.
pars 1994 *Hypagnostus brevifrons* (Angelin); Robison, p. 40, figs 15:4, 5.
pars 1994 *Peratagnostus cicer* (Tullberg); Robison, p. 67, fig. 34:1, 2 only.
1994 *Svenax confluentus* n. sp. Rudolph, p. 136, pl. 8, figs 4–5; textfig. 87.
1997 *Scanagnostus confluentus* (Rudolph); Buchholz, p. 207, pl. 3, fig. 3; textfig. 8A.
1997 *Scanagnostus trituberculatus* n. sp. Buchholz, p. 208, pl. 2, fig. 1; pl. 3, fig. 2; textfig. 8B.
1997 *Scanagnostus exiguus* n. sp. Buchholz, p. 210, pl. 2, fig. 2; textfig. 8C.
?1997 *Scanagnostus ornatus* n. sp. Buchholz, p. 244, pl. 2, fig. 3; pl. 3, fig. 1; textfig. 8D.
2000 *Lisogoragnostus hybus* new species Peng & Robison, p. 65, fig. 47.
2008 *Lisogoragnostus confluentus* (Rudolph); Høyberget & Bruton, p. 68, pl. 11, figs V, W.

Holotype (OD). – Pygidium, G 134/5, illustrated by Rudolph (1994, pl. 8, fig. 4) from the Andrarum Limestone Bed (lower part of the *L. laevigata* Zone). It was found in an ice-rafted boulder at Mucheln, Schleswig-Holstein, northern Germany, and is kept in the collection of the Museum 'Urzeithof' at Stolpe, Schleswig-Holstein, Germany.

Material and occurrence. – We found one complete specimen (Fig. 42A) at Abborrfallet, northern Jämtland, in the lower part of the *L. laevigata* Zone. Elsewhere in Scandinavia, the species is rare, but it has probably to some extent been overlooked because of its minute size. One pygidium from the Andrarum Limestone at Andrarum, Scania, was figured by Westergård (1946) as *Phalacroma* sp. Høyberget & Bruton (2008) figured one cephalon and one pygidium from the lower part of the *L. laevigata* Zone at Gran, Norway. Rudolph (1994) figured the holotype pygidium and Buchholz (1997) figured three pygidia found in ice-rafted boulders of the Andrarum Limestone on the island of Rügen, Germany. A comparatively large material of *L. confluentus*, comprising 25 specimens, has been collected by H.-J. Schmütz from boulders of the Andrarum Limestone Bed at the shore between Brantevik and Gislövshammar, Scania. Some of these specimens are illustrated herein to provide a better documentation of the species.

The three cephala and five pygidia illustrated by Rasetti (1967) as *Hypagnostus parvifrons* and Agnostida, pygidium no. 1 from the Taconic Sequence of New York originate from strata corresponding to the *P. forchhammeri* Superzone and undoubtedly belong to *L. confluentus*. Robison (1994) figured two cephala and two pygidia from the *L. laevigata* Zone on Greenland (as *Hypagnostus brevifrons* and *Peratagnostus cicer*) and also these specimens represent *L. confluentus*. The most abundant material reported so far (75 cephala and pygidia) was collected from the *L. laevigata* Zone in China (Peng & Robison 2000).

Description. – *Lisogoragnostus confluentus* is minute and one of the smallest agnostoids found in Scandinavia. Adult cephala and pygidia are generally about 1 mm long and wide but one exceptionally large pygidium is 2 mm long (Fig. 42N–P). Until now, the species was known only from a few detached cephala and pygidia, making determination unsafe. However, the complete specimen from Abborrfallet (Fig. 42A) provides safe evidence for combination of cephalon and pygidium of this species.

The cephalon is rounded and about as wide as long. Contrary to most other species of *Lisogoragnostus*, it possesses a distinct and narrow border and border furrow all around (Fig. 42H, I). The anteroglabella is effaced, the posteroglabella is elliptical, elevated above the cheeks and bounded by a deep furrow and carries a weak rounded node just in front of glabellar midpoint (Fig. 42B). The posterior end of the glabella extends behind the posterior end of the cheeks. The basal lobes are simple and of medium size. The pygidium is subcircular in outline. The acrolobe is merged with the border, which is the characteristic feature of *Lisogoragnostus*. The pleural fields are gently expanding rearwards, reaching maximum width approximately level with the tip of the axis, merging smoothly behind the axis; in young specimens this area is slightly depressed (Fig. 42J). The axis is highly inflated, tapers gently, and ends mostly slightly pointed, rarely roundedr. It carries a barely visible elongate node on M2 and a distinct terminal node, which sometimes has a little depression just in front (Fig. 42J, K, M). In larger holaspids, F1 and F2 are vaguely indicated (Fig. 42M, N). In most specimens, irrelevant of their size, the axis is widest at M1 (Fig. 42J, K, L, M, N), in others the axis is slightly inflated laterally and widest midlength of the posteroaxis (Fig. 42Q, R).

Remarks. – In the illustrated material of *L. hybus* from China, Peng & Robison (2000, fig. 47:1–9) show minor variation in the cephalon, namely in the length of the glabella relative to the total cephalic length and in the length/width ratio of the head shield. Similar variations are also seen in the Swedish material. However, the cephalon of *L. hybus* seems to be slightly more elongate in shape than *L. confluentus.* While the cephala from Lapland and Scania have an elliptical posteroglabella, Peng & Robison (2000) demonstrate variation in its shape, being in part elliptical (fig. 47: 1–3), in part truncate (fig. 47:4–5). The pygidial axis in the Chinese specimens have a rounded or slightly pointed tip, just like our specimens, but the axes are a bit wider than in the majority of the Scandinavian specimens and attain their greatest width at midlenght of the posteroaxis. Summarized, *L. confluentus* and *L. hybus* are distinct from all other species of *Lisogoragnostus*. Both species have similar minor variations in the same diagnostic traits and in the two obvious differences, a slightly more elongate cephalon and a more laterally inflated pygidial posteroaxis in *L. hybus*, specimens are found within *L. confluentus* and *L. hybus* that build a bridge to the other.

The three cephala and five pygidia from the Taconic Sequence (Rasetti 1967) are all typical *confluentus*-like. All cephala have an elliptical glabella – like in *confluentus* – and a preglabellar field of variable length – long like in *hybus*, and shorter like in *confluentus*. Four pygidia have a pointed axis with a distinct terminal node, like in *confluentus*, one has a laterally inflated axis which is widest midlenght of the posteroaxis, like in *hybus*. These illustrated specimens, clearly different from the specimens from China, were treated as synonyms of *L. hybus* by Peng & Robison (2000) and, accordingly, as intraspecific variations. Material from Greenland (Robison 1994), also synonymized with *L. hybus* by Peng & Robison (2000), show both in cephala and pygidia even more distinct the *confluentus*-like characters. In their treatment of *Lisogoragnostus*, Peng

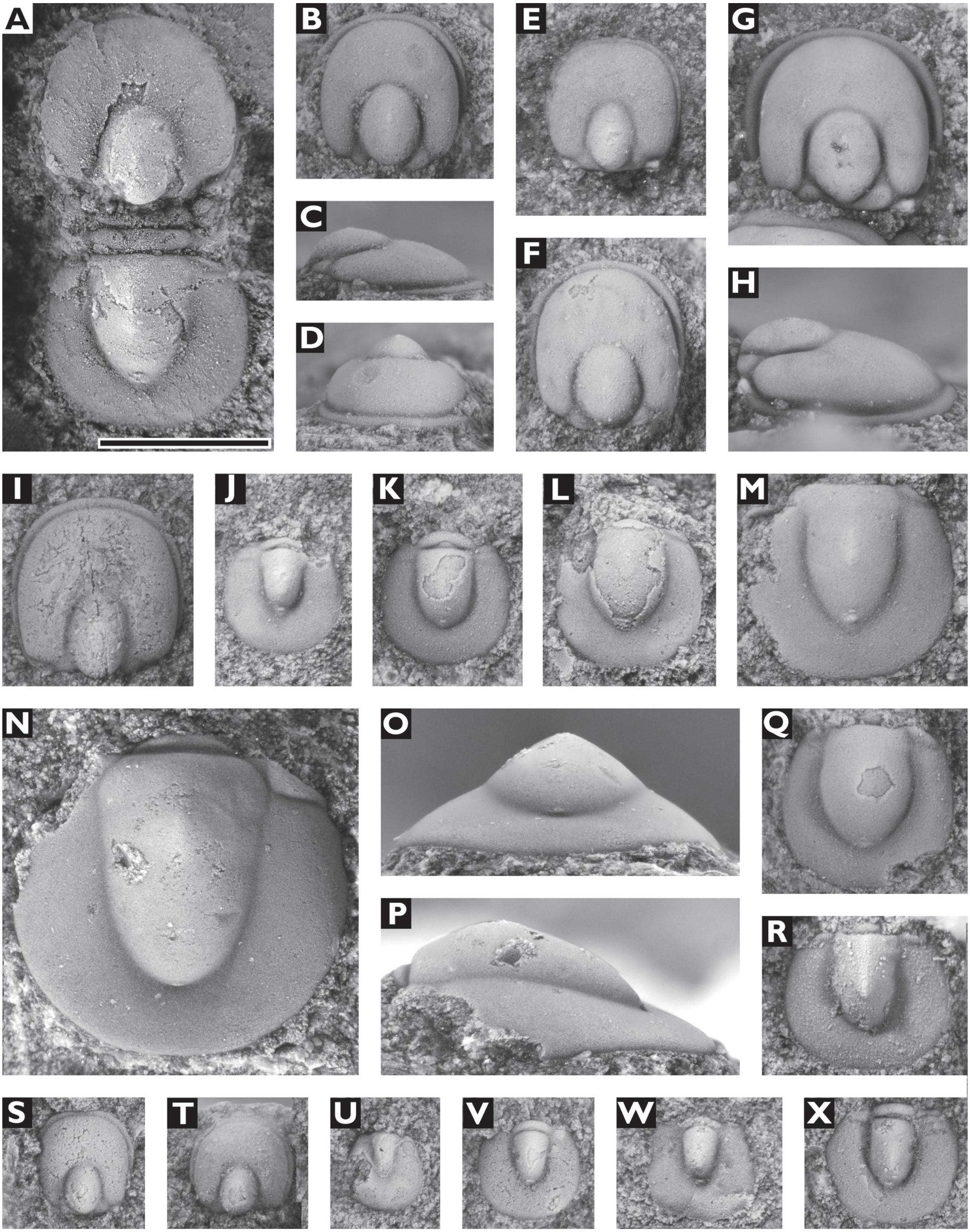


Fig. 42. ***Lisogoragnostus confluentus*** **(Rudolph, 1994)**, from the lower part of the *L. laevigata* Zone. **A**, complete specimen from Abborrfallet. PMU 26589/2. **B–I** and **S–T** are cephala and **J–R** and **U–X** are pygidia from the Andrarum Limestone Bed between Brantevik and Gislövshammar, Scania. B–D, dorsal, lateral and anterior views, PMU 35666/1. E, 35683/1. F, 35667/1. G–H, dorsal and lateral views, PMU 35668. I, 35677/2. J, 35682. K, 35667/2. L, 35680/1. M, showing the elongate axial node and the terminal node, 35672. N–P, dorsal, posterior and lateral views. F1 and F2 are vaguely indicated, 35671. Q, 35666/2. R, 35667/3. S, 35673/2. T, 35674/1. U, 35675/1. V, 35677/1. W, 35678. X, 35674/2. Scale bar = 1 mm. Note that the magnification is significantly larger than used for most agnostoid illustrations in this publication.

& Robison (2000) do not mention *Svenax confluentus*, Rudolph 1994, so the authors may have overlooked that publication. *Lisogoragnostus confluentus* and *L. hybus* come from the same stratigraphical level, i.e. the lower part of the *L. laevigata* Zone. We fully agree with Peng & Robison (2000) that the observed differences within and between the populations in Scandinavia and China are of intra-specific nature and we consider *hybus* as a junior synonym of *confluentus*. The species occurs in Sweden and Norway, Greenland, Laurentian North America and China, everywhere of latest Miaolingian age.

Buchholz (1997) erected *L. trituberculatus* and *L. exiguus*, based on one pygidium each, from boulders of the Andrarum Limestone Bed. However, the separating characters vary in larger materials of *L. confluentus* and we consider the two names as junior synonyms. *Lisogoragnostus ornatus* (Buchholz, 1997), also based on a single pygidium but from the older *P. punctuosus* Zone, and probably originating from the Bornholm area, seems to represent *L. confluentus* as well and, if the determination is correct, extends its stratigraphical range.

Shergold and Sdzuy (1984, p. 73, pl. 3, fig. 31) describe a single cephalon (as *Agnostinarum* gen. et sp. indet.) from the Furongian at Sultan Dag, central Turkey. The cephalon is of minute size, has a narrow border furrow, an elliptical glabella, and the posterior end of the glabella extends behind the posterior end of the cheeks and it likely represents *L. confluentus*.

Family uncertain

Genus *Glaberagnostus* Romanenko, 1985

Type species (OD). – *Glaberagnostus altaicus* Romanenko, 1985, from the *Glyptagnostus reticulatus* Zone, Furongian, Gorny Altay, Russia.

Diagnosis. – See Peng & Robison (2000).

Remarks. – *Toragnostus* Robison, 1988 (with *Agnostus bituberculatus* Angelin as type species) was erected for effaced agnostoids with an elongate node far forward from the cephalic midpoint. It was later ranked as a junior synonym of *Glaberagnostus* by Peng & Robison (2000).

Two species from the Miaolingian of Scandinavia are assigned to *Glaberagnostus*, viz. *G. bituberculatus* (Angelin, 1851) and *G. altaicus* Romanenko, 1985, and another two, *G.*? *forfex* (Brøgger, 1878) and *G.*? *cicer* (Tullberg, 1880), are tentatively assigned. For comments on the latter two species, see remarks on *G. bituberculatus* and *G.? cicer*.

Glaberagnostus bituberculatus (Angelin, 1851)

Figure 43A–F

1851 *Agnostus bituberculatus* n. sp. Angelin, p. 6, pl. 6, fig. 2.
non 1878 *Agnostus bituberculatus* Angelin; Brøgger, p. 75, pl. 6, fig. 9a, b [= *Cotalagnostus confusus*].
1902 *Agnostus glandiformis* Angelin; Grönwall, p. 63, pl. 1, fig. 6.
1930 *Agnostus bituberculatus* Angelin; Westergård *in* Holm & Westergård, p. 11, pl. 1, figs 10–12; pl. 4, figs 4–6.
1936 *Phoidagnostus bituberculatus* (Angelin); Whitehouse, p. 93 [*Phoidagnostus* erected].
1940 *Phoidagnostus bituberculatus* (Angelin); Lermontova, p. 130, pl. 36, figs 6, 6a–d.
1946 *Phoidagnostus bituberculatus* (Angelin); Westergård, p. 91, pl. 14, figs 10–14.
1953 *Phoidagnostus bituberculatus* (Angelin); Ivshin, p. 25, pl. 1, figs 1–9.
1958 *Phoidagnostus bituberculatus* (Angelin); Pokrovskaya, p. 39, pl. 3, figs 13, 14.
1960 *Phoidagnostus bituberculatus* (Angelin); Pokrovskaya *in* Tchernysheva, pl. 1, figs 24, 25.
1964 *Phoidagnostus bituberculatus* (Angelin); Rozova, p. 19, pl. 3, figs 13–20.
1968 *Phalagnostus bituberculatus* (Angelin); Palmer, p. B32, pl. 6, fig. 13.
pars 1975 *Phoidagnostus bituberculatus* (Angelin); Repina, Petrunina & Hajrullina, p. 119, pl. 11, figs 15–18; *non* fig. 19 [= ?*Glaberagnostus*? *cicer*].
1977 *Phoidagnostus bituberculatus* (Angelin); Romanenko, p. 168, pl. 23, figs 23, 24.
1982 *Phoidagnostus bituberculatus* (Angelin); Egorova *et al.*, p. 76, pl. 15, fig. 5.
1988 *Toragnostus bituberculatus* (Angelin); Robison, p. 53 [*Toragnostus* erected], fig. 12:4–6.
1990 *Toragnostus bituberculatus* (Angelin); Shergold, Laurie & Sun, fig. 18:7a, b.
pars 1991 *Phoidagnostus bituberculatus* (Angelin); Yang *et al.*, p. 119, pl. 7, figs 15–?16; pl. 8, fig. ?1; *non* fig. 2 [= *Glaberagnostus*? *cicer*].
1994 *Toragnostus bituberculatus* (Angelin); Robison, p. 72, fig. 37.
1994 *Toragnostus bituberculatus* (Angelin); Rudolph, p. 152, pl. 10, fig. 5.
1997 *Toragnostus bituberculatus* (Angelin); Shergold & Laurie, fig. 239:1a, b.
2000 *Glaberagnostus bituberculatus* (Angelin); Peng & Robison, p. 91, fig. 76.
2002 *Toragnostus bituberculatus* (Angelin); Schöning, fig. 11.
2010 *Glaberagnostus bituberculatus* (Angelin); Buchholz, pl. 2, fig. 11.

Neotype (designated by Shergold & Laurie 1997). – Cephalon, NRM Ar9563a, figured by Westergård in Holm & Westergård (1930, pl. 4, fig. 4) and refigured by Westergård (1946, pl. 14, fig. 10) and Shergold & Laurie (1997, fig. 239:1a). It derives from the Andrarum Limestone Bed, Andrarum, Scania, Sweden.

Material and occurrence. – The new material of *G. bituberculatus* was found at Siljeåsen and Abborrfallet in northern Jämtland in the lower part of the *L. laevigata* Zone. The species has been reported from the lower part of the *L. laevigata* Zone at various localities in Scania (Westergård 1946) and it occurs sparsely in the upper part of this zone at Menigasker in Närke (main collection at SGU; collection TW, unpublished). The species is further known from the lower part of the *L. laevigata* Zone on Bornholm, Denmark (Grönwall 1902) and from ice-rafted boulders found in northern Germany (Buchholz 2010). Elsewhere is the species reported from Alaska (Palmer 1968), Greenland (Robison 1988, 1994), Siberia (Westergård in Holm & Westergård 1930; Rozova 1964), Kazakhstan (Ivshin 1953), Turkestan (Repina 1975) and China (Peng & Robison 2000). Occurrence is everywhere in the *L. laevigata* Zone or equivalent strata.

Remarks. – *Glaberagnostus bituberculatus* is easy to recognize despite being effaced. The cephalon is rounded, slightly elongate, strongly convex and carries an elongate node far forward, which is a quite unusual character in agnostoids (Peng & Robison 2000). It lacks borders and furrows, except for the occasional presence of axial furrows surrounding the posterior end of M1. The small basal lobes are well-defined. The pygidium is smaller than the cephalon (Peng & Robison 2000). The effaced pygidial axis has an elongate node close to the anterior margin and the border furrow is channel-like, wide and deep (Rudolph 1994), and this seems to be another characteristic trait of *Glaberagnostus*. For additional taxonomic details, see Westergård (1946) and Robison (1988, 1994). Our material corresponds completely with that from Greenland (Robison 1994), China (Peng & Robison 2000) and Siberia (Rozova 1964).

One pygidium of *G. altaicus* has been reported from the upper part of the *L. laevigata* Zone at Gudhem in Västergötland (Axheimer *et al*. 2006). The German collector H.-J. Schmütz has found another pygidium at the same locality and stratigraphic level (PMU 37516) and one additional pygidium in the Andrarum Limestone Bed at Brantevik, Scania (PMU 37071). The cephalon of *G. altaicus* in the Chinese material described by Peng & Robison (2000) seems indistinguishable from that of *G. bituberculatus* whereas the pygidium differs by having the axial furrows partially outlined for approximately 70–90% of the axial length. Naimark & Pegel (2017) noted as a characteristic feature of the pygidium a small indentation at the rear, affecting the border, border furrow and acrolobe. This feature is seen in most of the specimens of *G. altaicus* illustrated from China (Peng & Robison 2000), and occasionally also in material from Scandinavia, but it has not been observed in *G. bituberculatus*. Hence, it does not seem be a constant character of the genus.

A cephalon of a complete specimen of *G.*? *forfex* (Brøgger, 1878) from the *L. laevigata* Zone in Norway, illustrated by Høyberget & Bruton (2008, pl. 11, fig. M) as *Glaberagnostus forfex*, shows a cephalon quite similar to those of *G. bituberculatus* and *G. altaicus*. However, this specimen is more rounded than ovate and the node is located behind cephalic midpoint and it cannot be assessed whether the node is rounded or moderately elongate. Two unpublished cephala from Norway (collection M. Høyberget) have a tiny rounded node in the same position, whereas a supposed cephalon of *G.*? *forfex* from Brantevik, Scania, shows an elongate node (PMU 35683/2) as in *G. bituberculatus* and *G. altaicus*. The pygidium of *G.*? *forfex* has axial furrows that are outlined slightly more posteriorly than in *G. altaicus* (approximately for 85–95% of the axial length), but the border furrow is narrow and the border is wide and flat, quite unlike the condition in *G. bituberculatus* and *G. altaicus*. However, two out of ten pygidia at hand from Norway and Sweden show the rear mesial indentation, described by Naimark & Pegel (2017) for *G. altaicus* (PMU 37069/1 & 37070). Høyberget & Bruton (2008) suggested modifying the diagnosis of *Glaberagnostus* in order to accommodate *G.*? *forfex* with the cephalic node situated behind the midpoint. We agree with Peng & Robison (2000) that the far forward position of the node is of major taxonomic importance, as this morphology is not seen in any other genera. Further, *G.*? *forfex* lacks the channel-like border furrow seen in the type species of *Glaberagnostus*. Hence, we assign *G. forfex* only tentatively to *Glaberagnostus*.

Glaberagnostus? *cicer* (Tullberg, 1880), ranging from the *P. punctuosus* Zone to the lower part of the *L. laevigata* Zone, has a cephalon that resembles *G. bituberculatus* in most features, but it is more rounded in outline, and not ovate as in *G. bituberculatus*, M1 is partially visible and the node is small and rounded and situated centrally. The pygidium differs from that of *G. bituberculatus* in having the axial furrows partially outlined and the axis carries a node that generally is elongate and seldom rounded. The indentation at the rear, as observed in *G. altaicus* and *G.*? *forfex*, is lacking. We here follow Peng & Robison (2000) in assigning the species only tentatively to *Glaberagnostus* due to the placement and shape of the cephalic node, which in *G. bituberculatus* and *G. altaicus* is located far forwards.

Megagnostus glandiformis (Angelin, 1851) from the lower part of the *L. laevigata* Zone differs from *G. bituberculatus* in attaining a much larger maximum size and in the effacement of the basal lobes on the cephalon and the apparent absence of a cephalic node (see, however, remarks on the species below). The pygidium differs in having a wide border of variable shape and an indistinct, rounded node on M2.

Other effaced agnostoids, like *Phalagnostus scanicus* (Tullberg, 1880) and *Valenagnostus marginatus* (Brøgger, 1878), possess a cephalic border and also the pygidial borders are quite different from *G. bituberculatus*.

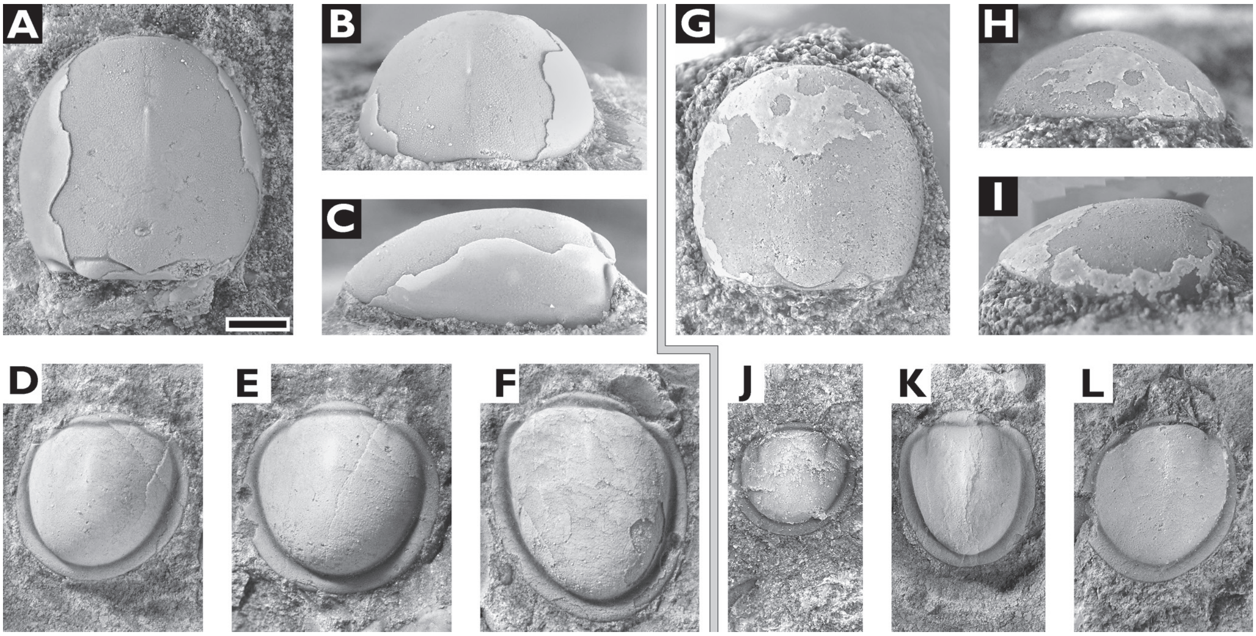


Fig. 43. ***Glaberagnostus bituberculatus*** **(Angelin, 1851)**. **A–C**, cephalon in dorsal, anterior and lateral views. Andrarum Limestone Bed, lower part of *L. laevigata* Zone at Brantevik, Scania. PMU 35689/1. **D–F**, pygidia, from Abborrfallet, lower part of the *L. laevigata* Zone. PMU 26596/1, 26575/1, 26596/2. In this species the pygidia are smaller than the cephala. ***Glaberagnostus*? *cicer*** **(Tullberg, 1880)**. **G–I**, cephalon in dorsal, anterior and lateral views. Andrarum Limestone Bed, lower part of *L. laevigata* Zone at Brantevik, Scania. PMU 35684. **J–L**, pygidia, from Abborrfallet, lower part of the *L. laevigata* Zone. PMU 26597/2, 26574/3, 26597/1. Scale bar = 1 mm.

Glaberagnostus*? *cicer **(Tullberg, 1880)**

Figure 43G–L

1880 *Agnostus cicer* n. sp. Tullberg, p. 26, pl. 2, figs 16a, b (illustrated upside down).
1883 *Agnostus cicer* Tullberg; Linnarsson, p. 32.
1902 *Agnostus cicer* Tullberg; Grönwall, p. 59.
1902 *Agnostus cicer* Tullberg, var. *forfex* n. var. Grönwall, p. 59 pl. 1, fig. 5.
1939 *Ciceragnostus cicer* Tullberg; Kobayashi, p. 134.
1946 *Ciceragnostus cicer* (Tullberg); Westergård, p. 90, pl. 14, figs 4–9.
1960 *Ciceragnostus cicer* (Tullberg); Pokrovskaya *in* Tchernysheva, pl. 1, fig. 29.
1962 *Ciceragnostus cicer* (Tullberg); Hutchinson, p. 89, pl. 10, figs 15, 16; pl. 11, figs 1, 2.
1967 *Ciceragnostus cicer* (Tullberg); Öpik, p. 76.
1982 *Ciceragnostus cicer* (Tullberg); Egorova *et al*., p. 73, pl. 18, fig. 1; pl. 19, fig. 4; pl. 23, fig. 3; pl. 54, fig. 8; pl. 61, figs 3, 4.
pars 1994 *Peratagnostus cicer* (Tullberg); Robison, p. 67, fig. 34:3–8; *non* fig. 34:1, 2 [= *Lisogoragnostus confluentus* (Rudolph, 1994)].
1994 *Grandagnostus cicer* (Tullberg); Rudolph, p. 148, pl. 10, figs 7–11.
2000 *Glaberagnostus*? *cicer* (Tullberg); Peng & Robison, p. 91, fig. 77.
2008 *Glaberagnostus cicer* (Tullberg); Høyberget & Bruton, p. 65, pl. 11, figs H–K.
2010 ?*Glaberagnostus cicer* (Tullberg); Buchholz, pl. 3, fig. 6.
2010 *Glaberagnostus cicer* (Tullberg); Buchholz, pl. 3, fig. 7.

Lectotype (designated by Westergård 1946). – Pygidium, LO 382t, originally illustrated by Tullberg (1880, pl. 2, fig. 16a–b) and refigured by Westergård (1946, pl. 14, fig. 4). It derives from the *P. punctuosus* Zone in the Alum Shale Formation at Andrarum, Scania, Sweden.

Material and occurrence. – *Glaberagnostus*? *cicer* has been found at Abborrfallet in the *P. punctuosus* Zone and at Siljeåsen, Abborrfallet and Fjällbränna in the lower part of the *L. laevigata* Zone. The species is known also from localities in Scania where it has a range from the *P. punctuosus* Zone into the lower part of the *L. laevigata* Zone (Westergård 1946). Rare specimens have been collected from ice-rafted boulders at As Hoved and Ulbjerg, Denmark, in a conglomeratic layer spanning the *P. punctuosus*/*G. nathorsti* zones (collection TW). Rudolph (1994) and Buchholz (2010) figured material from the *P. punctuosus* Zone and lower part of the *L. laevigata* Zone collected from ice-rafted boulders in northern Germany. In Scandinavia, the species is known also from Norway (Høyberget & Bruton 2008) and Bornholm, Denmark (Grönwall 1902). Elsewhere the species occurs in eastern Newfoundland (Hutchinson 1962), Siberia (Egorova *et al*. 1982), China (Peng & Robison 2000) and Greenland (Robison 1994). It has a range from the *P. punctuosus* Zone into the lower part of the *L. laevigata* Zone.

Remarks. – The species is infrequent in Sweden and only a few specimens have been illustrated (Westergård 1946; Rudolph 1994; Høyberget & Bruton 2008; Buchholz 2010). All figured cephala are rounded in overall outline, have no border or furrows and carry a tiny, rounded node placed centrally. The posterior part of M1 is partially discernible. The few pygidia illustrated show variation in several features: the partially outlined axial furrows may be slightly divergent posteriorly, tapering or straight and they may differ in length; the axial node can be rounded or elongate, prominent or indistinct; the border furrow can be narrow, moderately wide or channel-like (Robison 1994, fig. 34; Rudolph 1994, pl. 10, fig. 9) as in *G. bituberculatus* and *G. altaicus*; the border is either downsloping or up-turned, in the latter case creating what Rudolph (1994) referred to as a channel-like border furrow. Our pygidia have short axial furrows. Pygidia from Greenland (Robison 1994, as *Peratagnostus cicer*) agree in most features with the pygidia from Sweden, but larger specimens have a more ovate shape, the axial furrows diverge more strongly rearwards, the axial node seems to extend further backwards and the border furrow is channel-like, as in *G. bituberculatus* and *G. altaicus*. Robison (1994) ascribed these differences to ontogenetic variability in the populations from Greenland and Sweden. Høyberget & Bruton (2008) considered the Greenland specimens as probably belonging to *Phalacroma* (see also Westrop *et al.* 1996).

In comparison with *G. bituberculatus*, the cephalon of *G.*? *cicer* differs in the rounded overall shape and in having a tiny, rounded node placed centrally. The cephalon of *G. bituberculatus* is more ovate and has an elongate node situated in the anterior third. The pygidium of *G.*? *cicer* has the axial furrows partially outlined – but rarely behind M2 – and a rounded or elongate node; in *G. bituberculatus* the axial furrows are effaced. *Glaberagnostus altaicus* has an ovate cephalic shape and an elongate node placed in front of the midpoint. Its pygidium shows vestiges of the axial furrows for ¾ of the axial length. *Glaberagnostus*? *forfex* has a cephalon similar to *G.*? *cicer*, except that an elongate node is placed behind the cephalic midpoint. The pygidia of the two species are very similar, but differ in the length of the axial furrows.

Genus *Megagnostus* Robison, 1994

Type species (OD). – *Agnostus glandiformis* Angelin, 1851, from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Diagnosis. – See Robison (1994).

Remarks. – One species, *M. glandiformis* (Angelin, 1851), is known from the Miaolingian of Scandinavia whereas *M.*? *resecta* (Grönwall, 1902) is tentatively assigned.

Megagnostus glandiformis (Angelin, 1851)

Figure 44A–D

1851 *Agnostus glandiformis* n. sp. Angelin, p. 5, pl. 6, fig. 1.
1878 *Agnostus glandiformis* Angelin; Brøgger, p. 74, pl. 6, fig. 7.
1880 *Agnostus glandiformis* Angelin; Tullberg, p. 29, pl. 2, fig. 20a–c.
1901 *Agnostus glandiformis* Angelin; Lindström, p. 37, pl. 1, fig. 7.
pars 1902 *Agnostus glandiformis* Angelin; Grönwall, p. 63; *non* pl. 1, fig. 6 [= *Glaberagnostus bituberculatus* (Angelin, 1851)].
non 1902 *Agnostus glandiformis* Angelin var. *resecta* n. var. Grönwall, p. 64; pl. 1, fig. 7 [= *Megagnostus*? *resecta* (Grönwall, 1902)].
?1916 *Agnostus glandiformis* Angelin; Illing, p. 414, pl. 31, fig. 2.
1930 *Agnostus glandiformis* Angelin; Westergård *in* Holm & Westergård, p. 10, pl. 1, figs 2–5; pl. 4, figs 1–3.
1935a *Grandagnostus glandiformis* (Angelin); Howell, p. 221 [*Grandagnostus* erected].
1940 *Grandagnostus glandiformis* (Angelin); Lermontova, p. 131, pl. 36, figs 7, 7a–j.
1946 *Phalacroma glandiforme* (Angelin); Westergård, p. 95, pl. 15, figs 3–17; pl. 16, figs 1, 2.
1958 *Phalacroma glandiforme* (Angelin); Pokrovskaya, p. 53, pl. 4, figs 1–6.
1960 *Phalacroma glandiforme* (Angelin); Pokrovskaya *in* Tchernysheva, pl. 1, figs 26, 27.
1964 *Phalagnostus glandiformis* (Angelin); Rozova, p. 17, pl. 2, figs 14–21; pl. 3, fig. 3.
1969 *Grandagnostus glandiformis* (Angelin); V. Poulsen, p. 7, fig. 7.
?1970 *Phalacroma glandiforme* (Angelin); Hajrullina, p. 17, pl. 1, fig. 14.
?1973 *Phalacroma glandiforme* (Angelin); Hajrullina, p. 48, pl. 3, fig. 15.
?1975 *Phalagnostus glandiformis* (Angelin); Repina, Petrunina & Hajrullina, p. 118, pl. 11, figs 20, 21.
1976 *Grandagnostus* sp.; Jago, p. 141, pl. 22, figs 1–5.
1976 *Grandagnostus glandiformis* (Angelin); Jago, p. 144, pl. 24, figs 1–5.
1979 *Phalacroma glandiforme* (Angelin); Neben & Krueger, pl. 117, fig. 25.
1982 *Phalacroma glandiforme* (Angelin); Egorova *et al.*, p. 74, pl. 22, ?fig. 6; pl. 23, ?fig. 5; pl. 49, fig. 1; pl. 55, figs 12–13; pl. 59, fig. 5; pl. 62, fig. 9.
1994 *Megagnostus glandiformis* (Angelin); Robison, p. 63 [*Megagnostus* erected], fig. 33.
1994 *Grandagnostus glandiformis* (Angelin); Rudolph, p. 149, pl. 10, figs 1, 2.
1996 *Megagnostus glandiformis* (Angelin); Westrop, Ludvigsen & Kindle, p. 826, fig. 25:1, 2, 5, 6.
2000 *Megagnostus glandiforme* (Angelin); Pegel, fig. 11:15.
2008 *Megagnostus glandiformis* (Angelin); Høyberget & Bruton, p. 67, pl. 11, figs R–U.
2014 *Megagnostus glandiformis* (Angelin); Bentley & Jago, p. 272, fig. 3N–O.
2016 *Megagnostus glandiformis* (Angelin); Pegel *et al.*, p. 39, pl. 10, figs 13, 14, 18.

Lectotype (designated by Westergård 1946). – Cephalon, NRM Ar2015e, illustrated by Westergård (1946, pl. 15, fig. 6). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden, and is assumed to be one of Angelin's (1851) syntypes.

Material and occurrence. – We have found two cephala and two pygidia at Långseleån in the lower part of the *L. laevigata* Zone. *Megagnostus glandiformis* occurs also at Vedjeön and Abborrfallet in northern Jämtland (Westergård 1946) and at Högnäsån on the Tåsjö Mountain. In northern Sweden, the species is rare, whereas it is fairly common at various localities in Scania. Otherwise it occurs in Norway (Høyberget & Bruton 2008), on Bornholm, Denmark (Grönwall 1902), in ice-rafted boulders of northern Germany (Rudolph 1994), in Siberia (Westergård *in* Holm & Westergård 1930; Pokrovskaya 1958; Egorova *et al.* 1982; Pegel 2000), the Turkestan range (Hajrullina 1970, 1973), on Greenland (V. Poulsen 1969; Robison 1994), in western Newfoundland (Westrop *et al.* 1996) and Australia (Jago 1976), everywhere in the *P. forchammeri* Superzone, mostly in the lower part of the *L. laevigata* Zone.

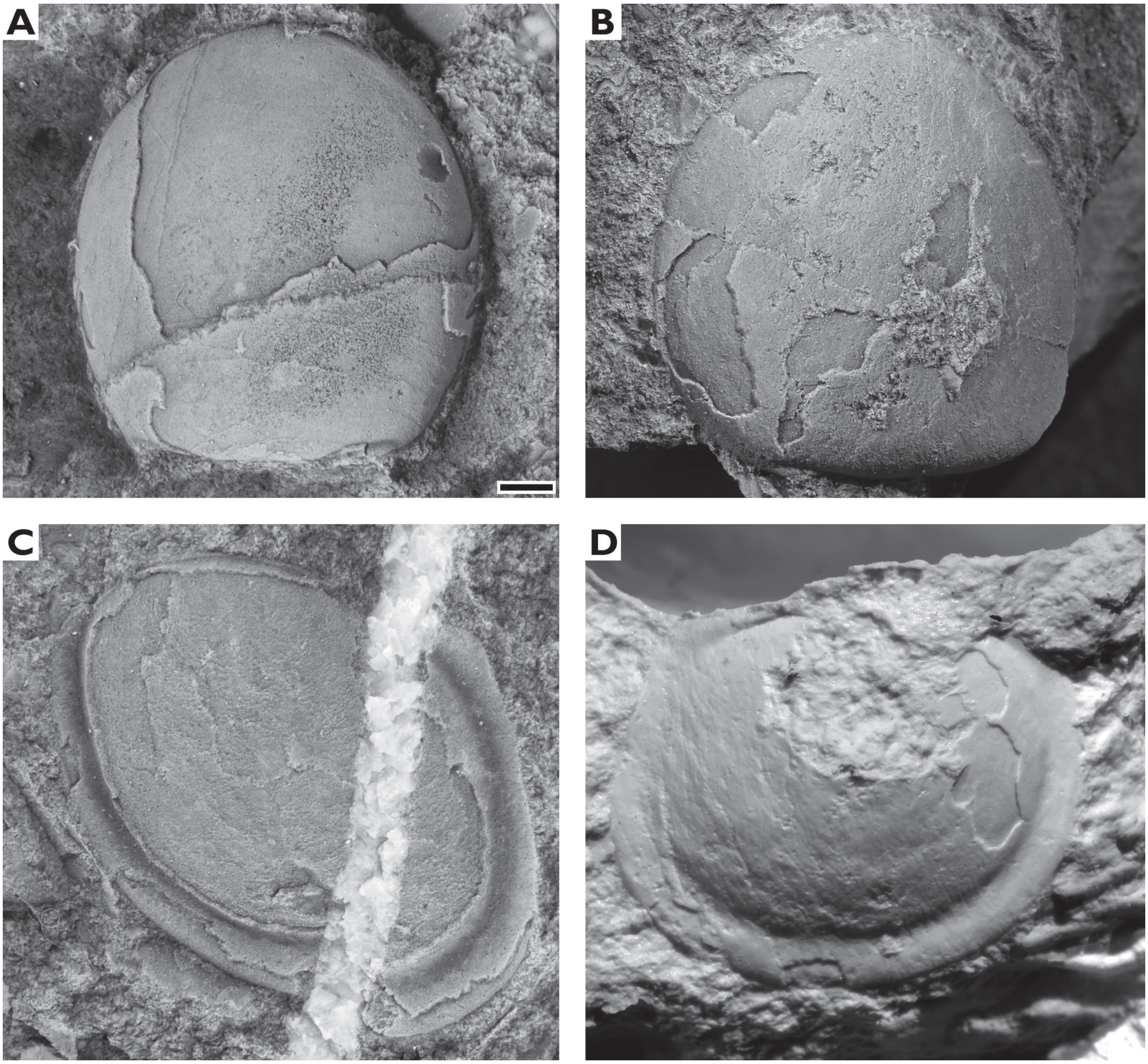


Fig. 44. ***Megagnostus glandiformis*** **(Angelin, 1851)**, from the lower part of the *L. laevigata* Zone. **A–B**, cephala, **C–D**, pygidia. A is from Vedjeön. SGU 9892. B is form Långseleån. PMU 37217a. C is from Högnäsån. PMU 26249/1. D is a plaster cast, from Långseleån. PMU 37217b/2. Scale bar = 1 mm.

Remarks. – *Megagnostus glandiformis* is the largest agnostoid occurring in Scandinavia with a length of either shield reaching 16 mm. The cephalon is completely effaced with no border, no furrows and no basal lobes; a centrally located glabellar lobe has been observed only once on an internal mould (Westergård, 1946. pl. 16, fig. 1), as noted by Høyberget & Bruton (2008). The pygidium has a wide border of almost even width throughout, the axial furrows are effaced and a small node is placed far forwards. The overall shape of both shields varies greatly. The material at hand is sparse and poorly preserved and we refer to the diagnosis and descriptions given by Westergård (1946), Robison (1994) and Høyberget & Bruton (2008).

Cephala of *M. glandiformis* differ from other agnostoid species without a border (like *Glaberagnostus*) in size, the mostly ovate shape, the effacement of even the basal lobes and the lack of a glabellar node. The pygidium resembles only that of *V. marginatus*, in which the border is narrow (see Westergård 1946, pl. 15, figs 9, 17 and Høyberget & Bruton 2008, pl. 12, figs I, J); see remarks on that species below.

Genus *Valenagnostus* Jago, 1976

Type species (OD). – *Agnostus nudus* Beyrich var. *marginata* Brøgger, 1878, from the *G. nathorsti* Zone, Alum Shale Formation at Krekling, Oslo Region, Norway.

Diagnosis. – See Shergold & Laurie (1997).

Remarks. – The assignment of various species to *Valenagnostus* was discussed by Peng & Robison (2000) and Høyberget & Bruton (2008). One species, *V. marginatus* (Brøgger, 1878), is described from the Miaolingian of Scandinavia.

Valenagnostus marginatus (Brøgger, 1878)

Figure 45A–O

1878	*Agnostus nudus* Beyrich var. *marginata* Brøgger, p. 73, pl. 6, fig. 3.
1880	*Agnostus nudus* Beyr. var. *marginatus* Brögger; Tullberg, p. 29, pl. 2, fig. 19.
1902	*Agnostus nudus* Beyr. var. *marginata* Brögger; Grönwall, pp. 62, 198.
1929	*Agnostus nudus marginatus* Brøgger; Strand, p. 346, pl. 1, fig. 8.
1946	*Phalacroma marginatum* (Brögger); Westergård, p. 94, pl. 14, figs 20–29; pl. 15, figs 1, 2.
1961	*Grandagnostus imitans* sp. nov. Öpik, p. 65, pl. 23, figs 12–15; pl. 24, figs 5–7; textfig. 20.
1961	*Grandagnostus velaevis* sp. nov. Öpik, p. 67, pl. 19, fig. 12; pl. 23, figs 3, 4; textfig. 21.
1967	*Grandagnostus evexus* sp. nov. Öpik, p. 86, pl. 52, figs 7–9.
1976	*Valenagnostus marginatus* (Brögger); Jago, p. 142, pl. 24, figs 6–9 [*Valenagnostus* erected].
1976	*Valenagnostus banksi* sp. nov. Jago, p. 147, pl. 22, figs 6–11; textfig. 1.
1976	*Valenagnostus brittoni* sp. nov. Jago, p. 148, pl. 23, figs 1–6.
1976	*Valenagnostus imitans* Öpik; Jago, p. 146.
1976	*Valenagnostus evexus* Öpik; Jago, p. 146.
1979	*Grandagnostus imitans* Öpik; Öpik, p. 73, pl. 22, fig. 4.
1990	*Valenagnostus marginatus* (Brögger); Shergold, Laurie & Sun, p. 57, fig. 18:6a, b.
1994	*Valenagnostus marginatus* (Brögger); Rudolph, p. 153, pl. 10, fig. 6.
1997	*Valenagnostus marginatus* (Brögger); Shergold & Laurie, p. 381, fig. 239:6a, b.
1999	*Valenagnostus marginatus* (Brøgger); Bruton, p. 341, fig. 4A–C.
2000	*Valenagnostus imitans* (Öpik); Peng & Robison, p. 96, fig. 80.
2008	*Valenagnostus imitans* (Öpik); Ergaliev & Ergaliev, p. 219, pl. 13, fig. 12; pl. 17, figs 18–23.
2008	*Valenagnostus marginatus* (Brøgger); Høyberget & Bruton, p. 70, pl. 12, figs D–J.
?2009b	*Valenagnostus imitans* Öpik; Peng *et al.*, p. 28, fig. 15:1–3.
2010	*Valenagnostus marginatus* (Brögger); Buchholz, pl. 3, figs 1, 4–5.

Lectotype (designated by Bruton 1999). – Mould of complete specimen, PMO 28114, figured by Bruton (1999, fig. 4A); assumed to be the original specimen illustrated by Brøgger (1878, pl. 6, fig. 3). It derives from the *G. nathorsti* Zone, Alum Shale Formation at Krekling, Oslo Region, Norway.

Material and occurrence. – In Västerbotten, *V. marginatus* was collected from the *G. nathorsti* Zone at Fjällbränna and Stendalsbäcken and reported by Kulling (1955) from the same zone at Skansholm. The species was also found in the lower part of the *L. laevigata* Zone at Siljeåsen, Abborrfallet and Karbäcken and reported from Lubbträsk by Kulling (1955). It is not possible to determine the zone for the reports of this species from Vedjeön, Hillsand, Brattbäcken and Ängesbäcken by Westergård (1946) and Kulling (1955). In Scania, Sweden, and on Bornholm, Denmark, the species is moderately common in the *G. nathorsti* Zone, but occurs sparsely also in the lower part of the *L. laevigata* Zone (Grönwall 1902; Westergård 1946). In Norway, it has been recorded in the *G. nathorsti* Zone and the lower part of the *L. laevigata* Zone (Brøgger 1878; Høyberget & Bruton 2008). The species has also been found in ice-rafted boulders of the Andrarum Limestone Bed in northern Germany (Rudolph 1994; Buchholz 2010). In Kazakhstan, it is recorded from the *L. laevigata* Zone (Ergaliev & Ergaliev 2008) and in Australia and China, it ranges from the same interval into the basal Furongian (Jago 1976; Peng & Robison 2000).

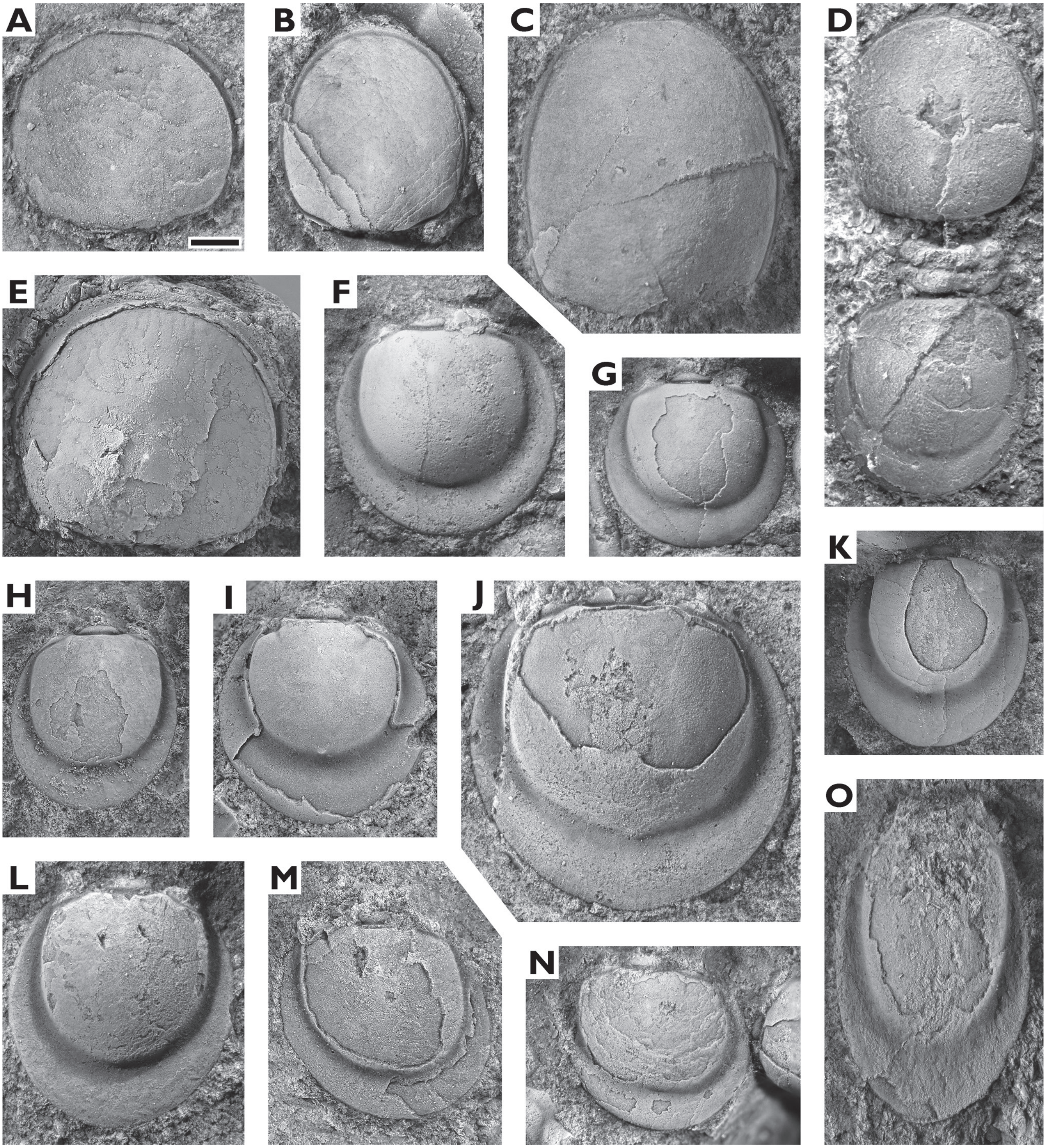


Fig. 45. ***Valenagnostus marginatus* (Brøgger, 1878)**. **A–C** and **E**, cephala. PMU 26604, 26586/2, 23066, 26591/1. **D**, complete specimen. PMU 37218. **F–O**, pygidia. PMU 26575/2, 26575/3, 29692/3, SGU 9902, PMU 26602, 26573/3, 23069, 26603, 26573/2, 23070/2. A–B, E–G, I–K and M–N are from Abborrfallet, lower part of *L. laevigata* Zone. C–D, L and O are from Stendalsbäcken, *G. nathorsti* Zone and H is from Fjällbränna, lower part of *L. laevigata* Zone. Scale bar = 1 mm.

Discussion. – Öpik (1961, 1967) and Jago (1976) erected several closely related species from Australia (viz. *Grandagnostus imitans, G. velaevis, G. evexus, Valenagnostus banksi* and *V. brittoni*). Jago (1976) transferred *G. imitans* and *G. evexus* to his newly erected genus *Valenagnostus*. These five species were distinguished by various minor cephalic and pygidial features observed on poorly preserved and tectonically deformed specimens (see Peng & Robison 2000, p. 95). Peng & Robison (2000) demonstrated, based on abundant, well-preserved material from China that the distinguishing features between these species are variable and overlap in larger populations. They accepted provisionally two taxa, *V. marginatus* from Scandinavia with a sagitally wide border, and *V. imitans* from Australia and China with a narrower border, which may, however, also just represent geographic variants. Ergaliev & Ergaliev (2008) figured material from Kazakhstan with a narrow border as *V. imitans*. Westergård (1946) noted variation in the length/width ratio of the cephalon and particular in the sagittal length of the pygidial border, but he considered these differences as 'individual variability'. Pygidia from Scandinavia, with a narrow border resembling the Chinese (Peng & Robison 2000, fig. 80:5–6) and Australian (Öpik 1961, pl. 24, figs 5–7) material were illustrated by Høyberget & Bruton (2008). These specimens co-occurred with pygidia having a wide border and were considered by them as conspecific. They regarded *V. marginatus* as the senior synonym and we agree with their interpretation.

All our new pygidia have a wide border, but the cephala exhibit variation with regard to the length/width ratio. Some are as wide as long (Fig. 45A, E), like those from Norway (Høyberget & Bruton 2008) and China (Peng & Robison 2000) and most Australian specimens (Öpik 1961; Jago 1976), others are about 10–15% longer than wide (Fig. 45B–D). Such relatively long forms have also been illustrated by Westergård (1946, pl. 15, fig. 1) and Jago (1976, pl. 22, figs 6, 7).

Two effaced species from Scandinavia, *Phalagnostus nudus* (Beyrich, 1845) from the *A. atavus* Zone and *Phalagnostus scanicus* (Tullberg, 1880) from the *P. punctuosus* Zone, resemble *V. marginatus*. The pygidia have a similar outline, the border is wider than in other agnostoids, but the *Phalagnostus* species have a distinct elongate node situated far forwards (see Weidner & Nielsen 2014, fig. 38C–F), while the node in *V. marginatus* is faint and rounded (Westergård 1946, pl. 15, fig. 2; Høyberget & Bruton 2008, pl. 12F, H). The only published cephalon of *P. scanicus* (Tullberg 1880, pl. 2, fig. 18; re-illustrated by Westergård 1946, pl. 14, fig. 15), has a narrow border as in *V. marginatus* but is otherwise totally effaced without any trace of a cephalic node, while *V. marginatus* shows a tiny, rounded node well behind midlength (Westergård 1946, pl. 15, fig. 1). Unlike that of *P. scanicus*, the cephalon of *P. nudus* lacks a cephalic border, and illustrated cephala of *P. nudus* (Šnajdr 1958) confirm the lack of a cephalic node.

Cephala of other effaced agnostoids like *Glaberagnostus bituberculatus, Glaberagnostus*? *cicer* and *Megagnostus glandiformis* differ from *V. marginatus* in having no cephalic border. The pygidium of *G. bituberculatus* has a narrow border and channel-like border furrow and an elongate node, whereas the pygidium of *G.*? *cicer* has partially developed axial furrows unlike *V. marginatus*. *Megagnostus glandiformis* is very large and the length/width ratio in both shields varies greatly. Pygidia of *M. glandiformis* are difficult to separate from those of *V. marginatus* with a narrow border, as both have a similar outline and a rounded node placed far anteriorly (see Westergård 1946, pl. 15, figs 9, 17 and Høyberget & Bruton 2008, pl. 12, figs I, J). In some cases only the associated cephala allow a reliable determination.

Family Eodiscidae Raymond, 1913

Genus *Eodiscus* Hartt *in* Walcott, 1884

Type species (OD). – *Eodiscus pulchellus* Hartt in Walcott, 1884, from the Fossil Brook Member of the Chamberlain's Brook Formation (*Eccaparadoxides eteminicus* Zone), New Brunswick, Canada. This level corresponds approximately to the Scandinavian *T. gibbus* Zone. Most authors, including Westergård (1946), Rasetti (1952), Hutchinson (1962) and Babcock (1994a), have considered *E. pulchellus* as a junior synonym of *Microdiscus scanicus* Linnarsson, 1883, from the lower part of the *A. atavus* Zone at Andrarum, Scania, Sweden, but Fletcher (2006) and provisionally also Westrop *et al.* (2018) classified it as a separate species due to possible differences in the surface ornamentation (see remarks).

Diagnosis. – See Rasetti (1952) and Jell (1997).

Remarks. – Differences in external and internal surface ornamentation – and whether these features vary within or between species – have been debated by Lake (1907), Westergård (1946) and Westrop *et al.* (2018). The latter authors were the first to invoke surface sculpture as a key taxonomic feature, which led them to erect new species based on material from Avalonian and Laurentian Newfoundland. They also held it likely that material from different parts of the world assigned to *Eodiscus punctatus* (Salter, 1864) in fact may represent several species. Museum collections in Scandinavia and Britain host a vast material assigned to the very common *E. punctatus* (Salter, 1864) and *E. scanicus* (Linnarsson, 1883), but illustrations are in general poor and few and mostly do not allow a detailed assesment of the surface sculpture. For this reason as well as the poor quality of the type material, Westrop *et al.* (2018) considered *E. punctatus* as a *nomen dubium*. The comparatively few illustrated Scandinavian specimens exhibit differences in the surface ornamentation during ontogeny and between different provinces, but this was not discussed by Høyberget & Bruton (2008) or Weidner & Nielsen (2014). The abundant *Eodiscus* material housed in various Scandinavian museums should be reinvestigated in order to reexamine this variation in view of the new approach to taxonomic classification proposed by Westrop *et al.* (2018). However, it is beyond the scope of this study to undertake such a reinvestigation and for the time being we maintain the traditional (broad) species concepts of *E. punctatus* (Salter, 1864) and *E. scanicus* (Linnarsson, 1883).

Eodiscus borealis Westergård, 1946 is a third species reported from the Miaolingian of Scandinavia. Together with *Eodiscus foveolatus* (Howell, 1935a, b) it differs from all other species of *Eodiscus* by having an *Eodiscus*-like cephalon and a *Dawsonia*-like pygidium. *Eodiscus borealis* was tentatively assigned to *Eodiscus* as cephalic characters were considered more important (Rasetti 1952).

***Eodiscus borealis* Westergård, 1946**

1946 *Eodiscus borealis* sp. n. Westergård, p. 23, pl. 1, figs 3–5.
1952 *Eodiscus borealis* Westergård; Rasetti, p. 449.
1966 *Eodiscus borealis* Westergård; Rushton, p. 26, pl. 3, figs 1–7; textfig. 10.
1982 *Eodiscus borealis* Westergård; Egorova *et al.*, p. 57, pl. 51, figs 12, 14.

Holotype. – Cephalon, SGU 4693, figured by Westergård (1946, pl. 1, figs 3–5). The specimen is from a boulder of the *T. gibbus* Zone at Vedjeön, northern Jämtland, Sweden.

Material and occurrence. – Six cephala and five pygidia from one single block were collected and illustrated by Westergård (1946). We did not find additional material and there are no other reports of this species from Sweden or Norway. It is reported from the *A. pinus* – *P. praecurrens* Zone of England by Rushton (1966) and from the lower part of the *A. atavus* Zone of Siberia by Egorova *et al.* (1982).

Remarks. – Westergård (1946) described the species in detail. The only well-preserved and illustrated cephalon of *E. borealis* is the holotype. Overall, it resembles *Eodiscus* and differs from Scandinavian specimens of *E. punctatus* and *E. scanicus* in having a slightly wider and rearwards narrowing border traversed by 40 distinct, straight furrows dividing the border into equally sized segments. This character recalls *Dawsonia oelandica* from Sweden, in which, however, the border is considerably wider. Cephala of *E. punctatus* and *E. scanicus* have a slightly narrower border of even width throughout and the border crenulation is indistinct and the 60-80 segments may rather appear as smaller or larger punctae. The pygidium differs clearly from *E. punctatus* and *E. scanicus* in having deep pleural furrows as in *Dawsonia*.

***Eodiscus punctatus* (Salter, 1864)**

Figure 24C, D

1864 *Microdiscus punctatus* spec. nov. Salter: 237, pl. 13, fig. 11a–c.
1883 *Microdiscus eucentrus* n. sp. Linnarsson, p. 30, pl. 4, figs 19, 20.
pars 1907 *Microdiscus punctatus* Salter; Lake, p. 36, pl. 3, figs 11, 12.
1946 *Eodiscus punctatus* (Salter); Westergård, p. 24, pl. 1, figs 12–15.
1952 *Eodiscus punctatus* (Salter); Rasetti, p. 448, pl. 53, figs 1–6.
1982 *Eodiscus punctatus* (Salter); Egorova *et al.*, p. 57, pl. 4, fig. 8; ?pl. 7, fig. 7; pl. 12, fig. 2; pl. 51, figs 9, 10; ?pl. 55, fig. 15.
1988 *Eodiscus punctatus* (Salter); Morris, p. 91.
1994 *Eodiscus punctatus* (Salter); Rudolph, p. 157, pl. 11, figs 4–7.
2008 *Eodiscus punctatus* (Salter); Høyberget & Bruton, p. 72, pl. 12, figs N–R.
2014 *Eodiscus punctatus* (Salter); Weidner & Nielsen, p. 67 (*cum syn.*), fig. 40A–I.

Lectotype (designated by Morris 1988). – Complete specimen, BMNH 42646, the original of Salter (1864, pl. 13, fig. 11a, b), from the Miaolingian at Porth-y-rhaw, near St Davids, Wales.

Material and occurrence. – Our two figured specimens are from the *P. punctuosus* Zone at Abborrfallet, northern Jämtland. Additional material from the same locality is housed at SGU. Elsewhere the species has been reported from Siljeåsen (northern Jämtland) and Scania (Westergård 1946), Norway (Høyberget & Bruton 2008), Bornholm (Weidner & Nielsen 2014) and ice-rafted boulders in northern Germany (Rudolph 1994). Outside Scandinavia, the species has been described from Great Britain (Thomas *et al.* 1984; Young *et al.* 2002; Rees *et al.* 2014), eastern Newfoundland (Hutchinson 1962; Fletcher 2006), northern Greenland (Poulsen 1969) and Siberia (Egorova *et al.* 1982). Occurrence is everywhere in the *A. atavus* and *P. punctuosus* zones.

Remarks. – In some of the exfoliated pygidia from southern Norway, assigned to *E. punctatus* by Høyberget & Bruton (2008), the external surface is punctate, while the surface of internal moulds is tuberculate. In another, smaller specimen, with a tuberculate external surface, the surface of the internal mould is punctate (see Høyberget & Bruton 2008, pl. 12, N–P versus Q). In well-preserved pygidia from Bornholm, the external surface is punctate with some tubercles adjacent to the axial furrows whereas smaller cranidia and one small pygidium have a tuberculate external surface; no internal mould are available (Weidner & Nielsen 2014). *Eodiscus tuberculus* and *E. confossus* figured by Westrop *et al.* (2018) differ from Scandinavian material in having both a punctate external and internal mould surface. For further comments on ornamentation, see remarks on genus.

Family Agraulidae Howell, 1937

Genus *Proampyx* Frech, 1897

Type species (OD). – *Proetus*? *difformis* var. *acuminatus* Angelin, 1851 from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Diagnosis. – See Weidner & Nielsen (2015a).

Remarks. – Four species described from the *L. laevigata* Zone of Scandinavia are assigned to *Proampyx*, viz. *P. difformis* (Angelin, 1851), *P. aculeatus* (Angelin, 1851), *P. acuminatus* (Angelin, 1851) and *P. anceps* (Westergård, 1953). Unpublished data from Magne Høyberget (personal communication 2016) indicate that a fifth species, *P. medianus* Sdzuy, 1966, occurs in the *G. nathorsti* Zone of the Oslo Region, Norway (see remarks on *Proampyx anceps*). *Proampyx*? *depressus* (Grönwall, 1902), recorded from the *P. punctuosus* Zone, is tentatively assigned. Only cranidia of these taxa have been published and they are distinguished by the length and shape of the frontal and occipital areas (Westergård 1953). Extensive unpublished material of *Proampyx* has been collected from the *G. nathorsti* Zone and the lower part of the *L. laevigata* Zone in southern Norway, including a complete specimen of *P. acuminatus*, pygidia of *P. aculeatus* and ontogenetic stages of *P. anceps* (Magne Høyberget personal communication 2016). Ahlberg & Bergström (1978) assigned several lower Cambrian species to *Proampyx*; these are now allocated to various other genera (e.g. Ahlberg & Bergström 1978; Geyer 1990; Geyer & Landing 2004; Geyer *et al.* 2004; Weidner & Nielsen 2015a; Høyberget *et al.* 2015; Cederström *et al.* 2022).

Proampyx difformis (Angelin, 1851)

Figure 46A

pars 1851 *Proetus*? *difformis* n. sp. Angelin, p. 22, pl. 18, fig. 5; *non* fig. 4 [= *Groenwallia microphthalma* (Angelin, 1851)].
1854 *Anomocare difforme* n. sp. Angelin, p. 25, pl. 18, fig. 5.
1878 *Arionellus difformis* (*Anomocare*) Angelin; Brøgger, p. 58, pl. 3, fig. 16.
1902 *Agraulos difformis* Angelin; Grönwall, p. 161.
1953 *Agraulos difformis* (Angelin); Westergård, p. 4, pl. 1, figs 1–8.
1978 *Proampyx difformis* (Angelin); Ahlberg & Bergström, p. 22, pl. 3, fig. 4.
1979 *Agraulos difformis* (Angelin); Neben & Krueger, pl. 117, fig. 18.
1994 *Proampyx difformis* (Angelin); Rudolph, pp. 182, 229, pl. 24, figs 8–10; textfig. 97.
1997 *Proampyx difformis* (Angelin); St. John & Babcock, p. 269, fig. 6A–B.
2010 *Proampyx difformis* (Angelin); Buchholz, pl. 2, fig. 3.
2015a *Proampyx difformis* (Angelin); Weidner & Nielsen, fig. 5J–N.

Lectotype (designated by Westergård 1953). – Cranidium, NRM Ar42824, illustrated by Westergård (1953, pl. 1, fig. 4). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Material and occurrence. – Cranidia of *Proampyx difformis* were found at Abborrfallet in northern Jämtland and at Högnäsån on the Tåsjö Mountain. The species is also known from Scania and Västergötland (Westergård 1953), Norway (Brøgger 1878), Bornholm, Denmark (Grönwall 1902), and from ice-rafted boulders in northern Germany (Rudolph 1994) and Denmark (Weidner & Nielsen 2015a). All occurences are in the lower part of the *L. laevigata* Zone, except for Krekling, Norway, where the species is reported also from the upper part of the *G. nathorsti* Zone. Elsewhere the species is described only from the *P. punctuosus* interval-Zone in Alaska (St. John & Babcock 1997).

Remarks. – The frontal area of *P. difformis* is generally shorter than in the other three Scandinavian species of *Proampyx* and is almost rounded, but there are specimens in which it is drawn out anteriorly and approaches *P. aculeatus*. *Proampyx difformis* has an occipital node, whereas *P. aculeatus* has an occipital node and a spine. Both *P. difformis* and *P. aculeatus* differ from *P. acuminatus* and *P. anceps*, which have the frontal area extended into a cusp. Our figured specimen has a damaged occipital ring, but as there is no indication of a broad spine base, we assign it to *P. difformis*.

Öpik (1961) stressed the similarity between the Australian species of *Proampyx agra* and *P. difformis*. *Proampyx agra* differs from *P. difformis* in the cranidium being much more effaced, having a parallel-sided glabella and wider fixed cheeks as well as a gently rounded cranidial front. *Proampyx difformis* has distinct axial and glabellar furrows, a tapering glabella, narrower fixed cheeks and greater variability in the cranidial front (from strongly rounded to pointed) (see also Weidner & Nielsen 2015a, p. 10).

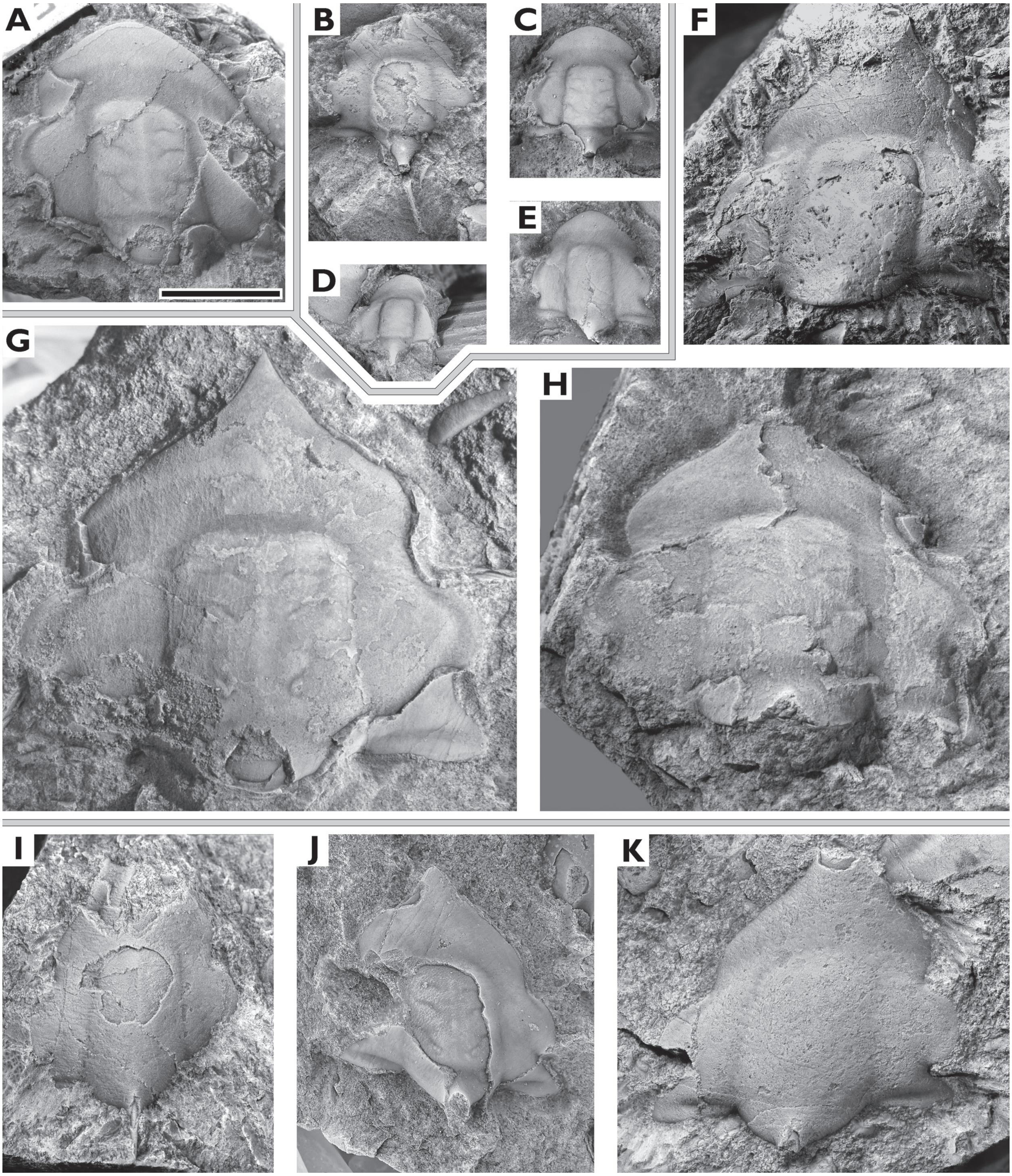


Fig. 46. Cranidia of ***Proampyx*** species. All are from the lower part of *L. laevigata* Zone. **A**, ***Proampyx difformis*** **(Angelin, 1851)**, from Abborrfallet. PMU 26570. **B–E**, ***Proampyx aculeatus*** **(Angelin, 1851)**, all from Abborrfallet. B, D–E are PMU 26586/1, 26572, 26587. C is SGU 9902. **F–H**, ***Proampyx acuminatus*** **(Angelin, 1851)**. PMU 37184/2, 26141/1, 26285. F is from Fjällbränna, G is from Vedjeön and H is from Högnäsån. **I–K**, ***Proampyx anceps*** **(Westergård, 1953)** from Fjällbränna, Vedjeön and Fjällbränna. PMU 37219, 26140/2, 37220/1. Scale bar = 5 mm.

Proampyx aculeatus **(Angelin, 1851)**

Figure 46B–E

1851 *Proetus*? *difformis* var. *aculeatus* n. sp. Angelin, p. 22, pl. 18, fig. 6.
1854 *Anomocare aculeatum* n. sp. Angelin, p. 26, pl. 18, fig. 6.
1878 *Arionellus difformis* var. *aculeata* (Angelin); Brøgger, p. 58, pl. 4, figs 1–8.
1902 *Agraulos difformis* var. *aculeata* Angelin; Grönwall, p. 161.
1953 *Agraulos aculeatus* (Angelin); Westergård, p. 5, pl. 1, figs 9, 10.
2013 *Proampyx difformis* (Angelin); Alvaro, Zamora, Vizcaïno & Ahlberg, p. 129, fig. 5a–f.

Lectotype (designated by Westergård 1953). – Cranidium, NRM Ar42828, illustrated by Westergård (1953, pl. 1, fig. 10). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – Cranidia of *P. aculeatus* were collected from the lower part of the *L. laevigata* Zone at Abborrfallet and Westergård (1953) has previously reported it from Siljeåsen. Elsewhere in Scandinavia, the species is known from the same zone in the Swedish provinces Scania, Öland and Västergötland (Westergård 1953), as well as from Bornholm, Denmark (Grönwall 1902), and various localities in Norway (Brøgger 1878). At Krekling, Norway, the species appears in the upper part of the *G. nathorsti* Zone (cf. Brøgger 1878). The only occurrence outside Scandinavia is in the upper Languedocian of the Montagne Noire, France (Álvaro *et al.* 2013).

Remarks. – Like *P. difformis*, *Proampyx aculeatus* has a variably developed frontal area, which affects the outline of the margin and the length of the border. The occipital ring bears a tiny node and a stout and long spine, which is the main difference from *P. difformis*. The tiny node is discernible in Figure 46B, C.

According to Westergård (1953), *P. difformis* is characterized by having an occipital ring with a node, whereas *P. aculeatus* has an occipital ring with a stout and long spine. He explicitly stated that the latter has a spine instead of a node. However, the two illustrated cranidia of *P. aculeatus* have a tiny occipital node, as well as an occipital spine that protrudes rearwards as an extension of the occipital ring (see also Brøgger 1878, pl. 4, fig. 4). Álvaro *et al.* (2013) synonymized *P. aculeatus* with *P. difformis*. They observed that in external moulds of the Iberian material the occipital node 'is extended into a prominent, posteriorly directed spine', and they inferred that the distinction of the two species is based on preservational effect (*ibid.* p. 129). However, specimens of *P. difformis* illustrated by Álvaro *et al.* (2013, fig. 5a–d) display an occipital node as well as an occipital spine that forms an extension of the occipital ring. Hence, we assign the specimens to *P. aculeatus* and maintain Westergård's (1953) distinction of *P. difformis* (with a small node on the occipital ring) and *P. aculeatus* (having a node and a spine).

Proampyx acuminatus **(Angelin, 1851)**

Figure 46F–H

1851 *Proetus*? *difformis* var. *acuminatus* n. sp. Angelin, p. 22, pl. 18, fig. 7.
1854 *Anomocare acuminatum* n. sp. Angelin, p. 26, pl. 18, fig. 7.
1897 *Proampyx acuminatus* (Angelin); Frech, p. 66.
1902 *Agraulos difformis* var. *acuminata* Angelin; Grönwall, p. 161.
pars ?1930 *Agraulos acuminatus* (Angelin); Westergård *in* Holm & Westergård, p. 19, pl. 3, fig. 18; *non* pl. 4, fig. 15 [= *Proampyx anceps*].
1953 *Agraulos acuminatus* (Angelin); Westergård, p. 6, pl. 1, figs 11–15.
1961 *Proampyx acuminatus* (Angelin); Öpik, p. 144.
1964 *Agraulos acuminatus* (Angelin); Rozova, p. 29, pl. 2, fig. 1.
1978 *Proampyx acuminatus* (Angelin); Ahlberg & Bergström, p. 22, pl. 3, fig. 3.
1982 *Agraulos acuminatus* (Angelin); Egorova *et al.*, p. 82, pl. 14, fig. 11; pl. 16, figs 1, 2; ?pl. 25, figs 6–8.
1994 *Proampyx acuminatus* (Angelin); Rudolph, p. 183, pl. 24, figs 6, 7.
1997 *Proampyx acuminatus* (Angelin); St. John & Babcock, p. 269, fig. 6C, D.

Lectotype (designated by Westergård 1953). – Cranidium, NRM Ar42830, illustrated by Westergård (1953, pl. 1, fig. 13). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Material and occurrence. – Cranidia of *P. acuminatus* were found in the lower part of the *L. laevigata* Zone at Vedjeön, at Högnäsån on the Tåsjö Mountain and at Fjällbränna. It has also been reported from Fånån and Abborrfallet (Asklund & Thorslund 1935; Westergård 1953). Elsewhere in Scandinavia, the species is known from the same zone in the Swedish provinces Scania and Västergötland (Westergård 1953), and it has also been found on Bornholm, Denmark (Grönwall 1902) as well as at several localities in Norway (personal communication Magne Høyberget 2016). Outside Scandinavia, the species occurs in the *L. laevigata* Zone of Siberia (Rozova 1964; Egorova *et al.* 1982) and the upper Miaolingian of Alaska, where it possibly turns up already in the *P. punctuosus* Zone (St. John & Babcock 1997).

Remarks. – *Proampyx acuminatus* is characterized in having the frontal area extended into a cusp, which mostly extends horizontally, but sometimes is slightly curved upwards, and it has an occipital ring with a node (Westergård 1953). Magne Høyberget (personal communication 2016) has found specimens of *P. acuminatus* at Gran, Norway, in which the cusp is curving upwards. Our specimens are poorly preserved, but the diagnostic criteria can be observed.

Proampyx anceps **(Westergård, 1953)**

Figure 46I–K

1930 *Agraulos acuminatus* (Angelin); Westergård *in* Holm & Westergård, p. 19, pl. 4, fig. 15.
1953 *Agraulos anceps* sp. n. Westergård, p. 6, pl. 2, figs 1–3.

Holotype (OD). – Cranidium, NRM Ar42829, figured by Westergård in Holm & Westergård (1930, pl. 4, fig. 15) and refigured by Westergård (1953, pl. 2, fig. 2). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Material and occurrence. – Three cranidia were found in the lower part of the *L. laevigata* Zone at Fjällbränna and one at Vedjeön in northern Jämtland. This infrequent species is also known from Scania (Westergård 1953). In Norway, the species has been collected from the *G. nathorsti* Zone (personal communication Magne Høyberget 2016).

Remarks. – *Proampyx anceps* differs from *P. acuminatus* in having a longer and distally more slender cusp at the front of the cranidium, which curves upwards, and the occipital ring carries a faint node as well as a spine. Westergård (1953) stated that *P. anceps* has a spine instead of a node, but his illustrated cranidium with preserved occipital ring shows a spine as well as a faint occipital node (Westergård 1953, pl. 2, fig. 1). This node can be observed also in unpublished material from Norway (personal communication Magne Høyberget 2016). *Proampyx aculeatus* has a similar occipital area as *P. anceps*, but lacks the cusp and has a wide and gently curved frontal margin instead. The new specimens show the frontal cusp and the occipital spine but the tiny node cannot be observed due to poor preservation.

Buchholz (1997, fig. 13A, pl. 15b) separated one fragmentary cranidium with an almost vertically erected cusp as *P. cornutus*. The specimen is from an ice-rafted boulder of the Andrarum Limestone Bed, from the lower part of the *L. laevigata* Zone, found at Boltenhagen, northern Germany. The occipital area is missing and this fragmentary cranidium probably represents *P. anceps* or *P. acuminatus*. Cusps turning upwards are not unusual and have been observed by Westergård (see *P. anceps*) and Høyberget (see *P. acuminatus*) and the vertical cusp in *P.* '*cornutus*' may just be an extreme variation.

Proampyx anceps medianus Sdzuy, 1966, from the Frankenwald, Germany, treated as *P. medianus* by Geyer *et al.* (2019), has narrower fixigenae than *P. anceps*. The same feature has been observed in material from Norway, suggesting that this species is present also in Scandinavia (personal communication Magne Høyberget 2016).

Family ?Andrarinidae Raymond, 1937

Genus *Groenwallia* Kobayashi, 1935

Type species (OD). – *Liostracus platyrrhinus* Grönwall, 1902, from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Borggård, Øleå, Bornholm, Denmark.

Diagnosis. – See Howell (1959).

Remarks. – Westergård (1953), Bruton *et al.* (1984) and Nikolaisen & Henningsmoen (1990) questioned the inclusion of *Groenwallia* in Andrarinidae.

Within Scandinavia, *G. microphthalma* (Angelin, 1851) and *G. platyrrhinus* (Grönwall, 1902) are recorded from the lower part of the *L. laevigata* Zone. *Groenwallia*? *angermanensis* Westergård, 1953, from the same level, is 'poorly preserved and possibly representing an immature form' and 'the absence of a definite border may even indicate generic distinction'. The only cranidium found was tentatively assigned to *Groenwallia* by Westergård.

Groenwallia microphthalma **(Angelin, 1851)**

Figure 47D–H

1851 *Proetus*? *microphthalmus* n. sp. Angelin, p. 22, pl. 18, fig. 4.
pars 1851 *Proetus*? *difformis* (Angelin); Angelin, p. 22, pl. 18, fig. 5 (pygidium only).
1854 *Anomocare microphthalmum* n. sp. Angelin, p. 25, pl. 18, fig. 4.
1873 *Liostracus microphthalmus* (Angelin); Linnarsson, p. 244.
1876 *Liostracus microphthalmus* (Angelin); Brøgger, p. 195, pl. 8, figs 4, 4a, b.
1878 *Liostracus microphthalmus* (Angelin); Brøgger, p. 48, pl. 3, figs 1, 2.
1902 *Liostracus microphthalmus* (Angelin); Grönwall, p. 146.

1929 *Loganellus microphthalmus* (Angelin); Strand, p. 354.
1953 *Grönwallia microphthalma* (Angelin); Westergård, p. 32, pl. 7, figs 13–17.
1984 *Groenwallia microphthalma* (Angelin); Bruton *et al*., p. 322, pl. 5, figs G–I, K, L.
1994 *Grönwallia microphthalma* (Angelin); Rudolph, p. 199, pl. 28, figs 16, 17.

Lectotype (designated by Westergård 1953). – Cranidium, NRM Ar46146, figured by Westergård (1953, pl. 7, fig. 13), from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – We found three pygidia of this species at Abborrfallet and Vedjeön in northern Jämtland, but also illustrate material from the same area kept in the main collection at SGU (Fig. 47D, G). Westergård (1953) reported the species also from Siljeåsen. In Sweden, *G. microphthalma* is further known from Scania, Öland, Västergötland and central and northern Jämtland (Westergård 1953). In Norway, it is reported from the Oslo Region (Brøgger 1878) and in Denmark from Bornholm (Grönwall 1902). It has also been found in ice-rafted boulders at As Hoved, Denmark (TW collection) and northern Germany (Rudolph 1994). All occurrences are from the lower part of the *L. laevigata* Zone, either Andrarum Limestone Bed or Exporrecta Conglomerate Bed.

Remarks. – *Groenwallia microphthalma* is endemic to Scandinavia. It is described and well-illustrated by Westergård (1953). The pygidia are readily identified in being twice as wide as long, having a narrow, tapering axis, distinct segmentation of the axis and pleural fields and a flat and wide border which widens considerably forwards.

Family Conokephalinidae Hupé, 1955

Genus *Conokephalina* Brøgger, 1886

Type species (SD, Bassler, 1915). – *Conocephalites ornatus* Brøgger, 1878, from the *P. punctuosus* Zone, Alum Shale Formation at Krekling, Oslo Region, Norway.

Diagnosis. – See Lochmann-Balk (1959).

Remarks. – Only one species, *C. ornata* (Brøgger, 1878), is known from the Miaolingian of Scandinavia. *Conokephalina suecica* (Wallerius, 1895) was transferred to *Westergaardella* by Kobayashi (1962, p. 77).

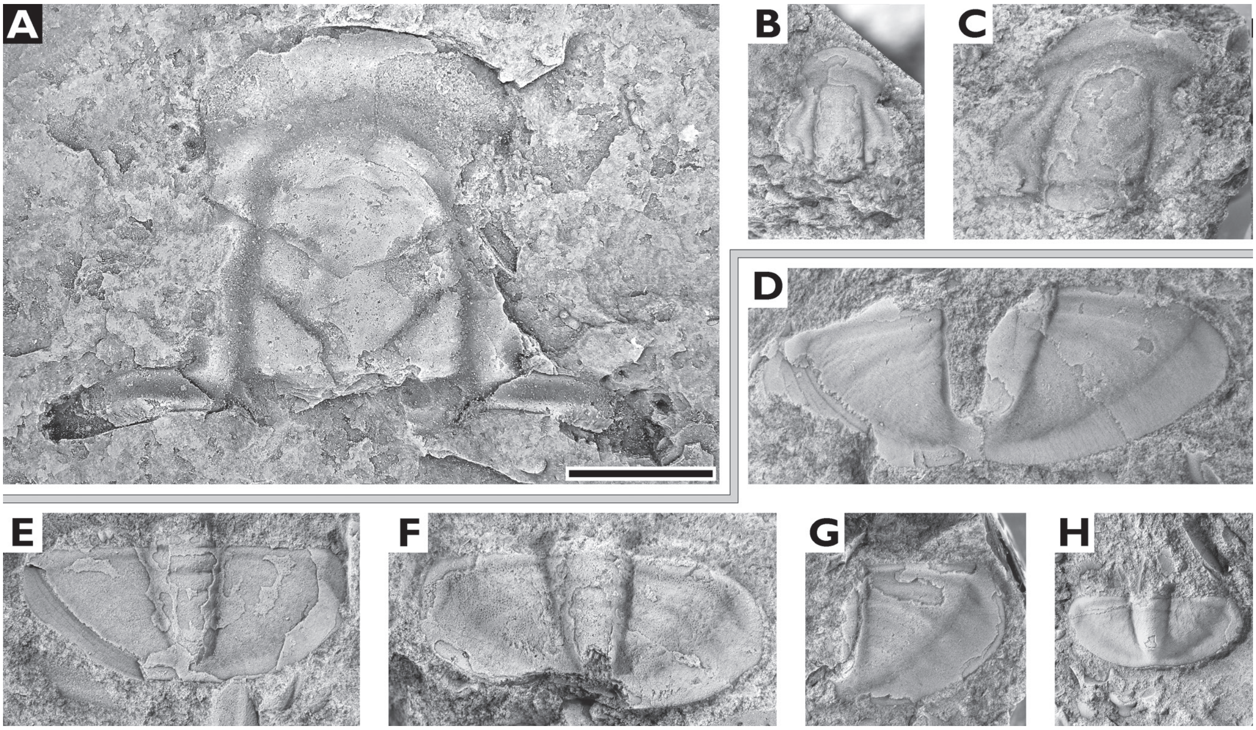


Fig. 47. ***Conokephalina ornata* (Brøgger, 1878)**, **A**, **lectotype** cranidium from the *P. punctuosus* Zone at Krekling, Norway. PMO H2687b. **B–C**, both cranidia are from the *P. punctuosus* Zone at Abborrfallet. PMU 34439, 26241. ***Groenwallia microphthalma* (Angelin, 1851)**, pygidia from the lower part of *L. laevigata* Zone. **D, G** from Abborrfallet. SGU 9910, SGU 9909. **E–F** from Vedjeön. PMU 26143/2, 26143/3. **H** from Abborrfallet. PMU 26606. Scale bar = 5 mm.

Conokephalina ornata (Brøgger, 1878)

Figure 47A–C

1878	*Conocephalites ornatus* n. sp. Brøgger, p. 53, pl. 3, figs 5, 6, ?7 (drawings).
1886	*Conocephalina ornatus* Brøgger; Brøgger, p. 206.
?1902	*Conokephalina ornata* (Brøgger); Grönwall, p. 150.
1914	*Conokephalina ornata* (Brögger); Walcott, p. 387, pl. 64, fig. 8 (drawing refigured).
1929	*Conokephalina ornata* (Brøgger); Strand, p. 355.
1958	*Conokephalina ornata* (Brögger); Šnajdr, p. 191.
1962	*Conokephalina ornata* Brögger; Kobayashi, p. 76, pl. 9, fig. 18.
1967	*Conokephalina ornata* (Brögger); Öpik, p. 247.
1994	*Conokephalina* cf. *ornata* (Brögger); Rudolph, p. 184, pl. 12, fig. 8.
2004	*Conokephalina ornata* (Brögger); Weidner, Ahlberg, Axheimer & Clarkson, p. 44.

Type material. – Kobayashi (1962, pl. 9, fig. 18) illustrated a plaster cast of a cranidium referred to as holotype. However, no holotype was appointed originally. This illustration is here taken as designation of a lectotype; according to Franz-Josef Lindemann, Oslo, the specimen has been identified as PMO H2687b, which is one of Brøgger's original syntypes of '*Conocephalites*' *ornatus*. It is here re-illustrated in Figure 47A.

Material and occurrence. – Two cranidia were found in the *P. punctuosus* Zone at Abborrfallet associated with *D. incertus* (see also Asklund & Thorslund 1935). Elsewhere, *C. ornata* is known from the '*P. rugolusus*' Zone (in either the uppermost part of the *P. punctuosus* Zone or the lowest part of the *G. nathorsti* Zone) in the Oslo region, Norway (Brøgger, 1878) and from Bornholm, Denmark (Grönwall 1902, not illustrated). The latter author also reported two specimens from the *G. nathorsti* Zone, but reworking cannot be excluded.

Remarks. – This rare trilobite is poorly known. Originally three cranidia (of which one was questionably assigned), one librigena and one pygidium were illustrated as drawings (Brøgger 1878) and since then only a plaster cast of one of the syntypes has been illustrated, see 'Type Material'. The two new cranidia are partially deformed, both have a weathered surface and they lack the posterior area of the fixigenae. Even so, they show the long, only slightly tapering, truncate glabella with three backwardly directed glabellar furrows, the narrow fixigenae and the long and curved palpebral lobes. The anterior border and the preglabellar furrow are both wide and of similar width. The occipital ring is slightly wider than indicated in Brøgger's drawings (1878, pl. 3, figs 5, 6), but the photo of the lectotype (Fig. 47A) shows that the occipital ring in fact is wider than outlined by Brøgger.

Conokephalina suecica from the upper part of the *L. laevigata* Zone differs from *C. ornata* in having a strongly tapering glabella which is rounded at front and shows only two pairs of glabellar furrows, the fixigenae have strongly curved palpebral lobes which are wider and the posterior area is considerably shorter (tr).

Rudolph (1994) figured a fragmentary cranidium of *Conokephalina* cf. *ornata* from the *P. punctuosus* Zone found in an ice-rafted boulder at Åbenrå, southern Denmark, which in his opinion deviates in the lengths of the preglabellar field and the occipital ring and possibly represents a different species. The comparison referred to Brøgger's drawings, but in fact his specimen matches well with the lectotype and our cranidia.

Family Paradoxididae Hawle & Corda, 1847

Remarks. – Fletcher *et al.* (2005) classified *Plutonides* Hicks, 1895, *Eccaparadoxides* Šnajdr, 1957 and *Hydrocephalus* Barrande, 1846 as subgenera of *Paradoxides* and considered *Acadoparadoxides* Šnajdr, 1957 and *Baltoparadoxides* Šnajdr, 1986 as junior synonyms of *Plutonides* based on similarities in the morphology of the glabellar furrows and palpebral lobes. Fletcher (2007) added *Mawddachites* as another subgenus. Geyer & Vincent (2014) pointed out that the type specimen of *Plutonides* is poorly preserved and they regarded the shared morphology to be of minor significance. Hence the classification by Fletcher *et al.* (2007) was rejected and this is followed here, where we rank *Baltoparadoxides* as a subgenus of *Acadoparadoxides* (cf. Dean & Rushton 1997; Geyer & Vincent 2014; Weidner *et al.* 2014; Rushton *et al.* 2016).

Genus *Acadoparadoxides* Šnajdr, 1957

Type species (OD). – *Paradoxides sacheri* Barrande, 1852, from the *Eccaparadoxides pusillus* Zone, Jince, Bohemia, Czechia.

Diagnosis. – See Dean & Rushton (1997).

Remarks. – We recognize two subgenera, *A.* (*Acadoparadoxides*) and *A.* (*Baltoparadoxides*), see remarks above on the Paradoxididae.

Subgenus *Acadoparadoxides* (*Acadoparadoxides*) Šnajdr, 1957

Type species (OD). – As for genus.

Diagnosis. – See Dean & Rushton (1997).

Remarks. – Only two species, *A.* (*A.*) *torelli* (Westergård in Asklund & Thorslund 1935) and *A.* (*A.*) *pinus* (Westergård 1936), are described from the Miaolingian of Scandinavia.

***Acadoparadoxides* (*Acadoparadoxides*) *torelli* (Westergård *in* Asklund & Thorslund 1935)**

Figure 48A–L

2014 *Acadoparadoxides torelli* (Westergård *in* Asklund & Thorslund); Weidner *et al.*, p. 519, figs 10–11 (authorship discussed; further synonymy).

2016 *Acadoparadoxides torelli* (Westergård *in* Asklund & Thorslund); Mannelqvist, p. 19, fig. 9:1, 4–5.

Lectotype (designated by Westergård 1936). – Almost complete specimen, SGU 705, from the '*Paradoxides oelandicus* Beds' (Bårstad Mbr, Borgholm Formation) in a well at Borgholm, Öland, Sweden. It was illustrated by Westergård (1936, pl. 8, figs 1a, b) and refigured by Weidner *et al.* (2014, fig. 10).

Material and occurrence. – Ten cranidia, one hypostome, two librigenae and two pygidia were found in the *A. pinus* – *P. praecurrens* Zone at Björnbäcken and Stendalsbäcken, at the latter locality associated with *P. praecurrens* (Weidner *et al.* 2014). *Acadoparadoxides* (*A.*) *torelli* also occurs in autochthonous strata at Kyrkberget, northwest of Storuman (Kulling 1982).

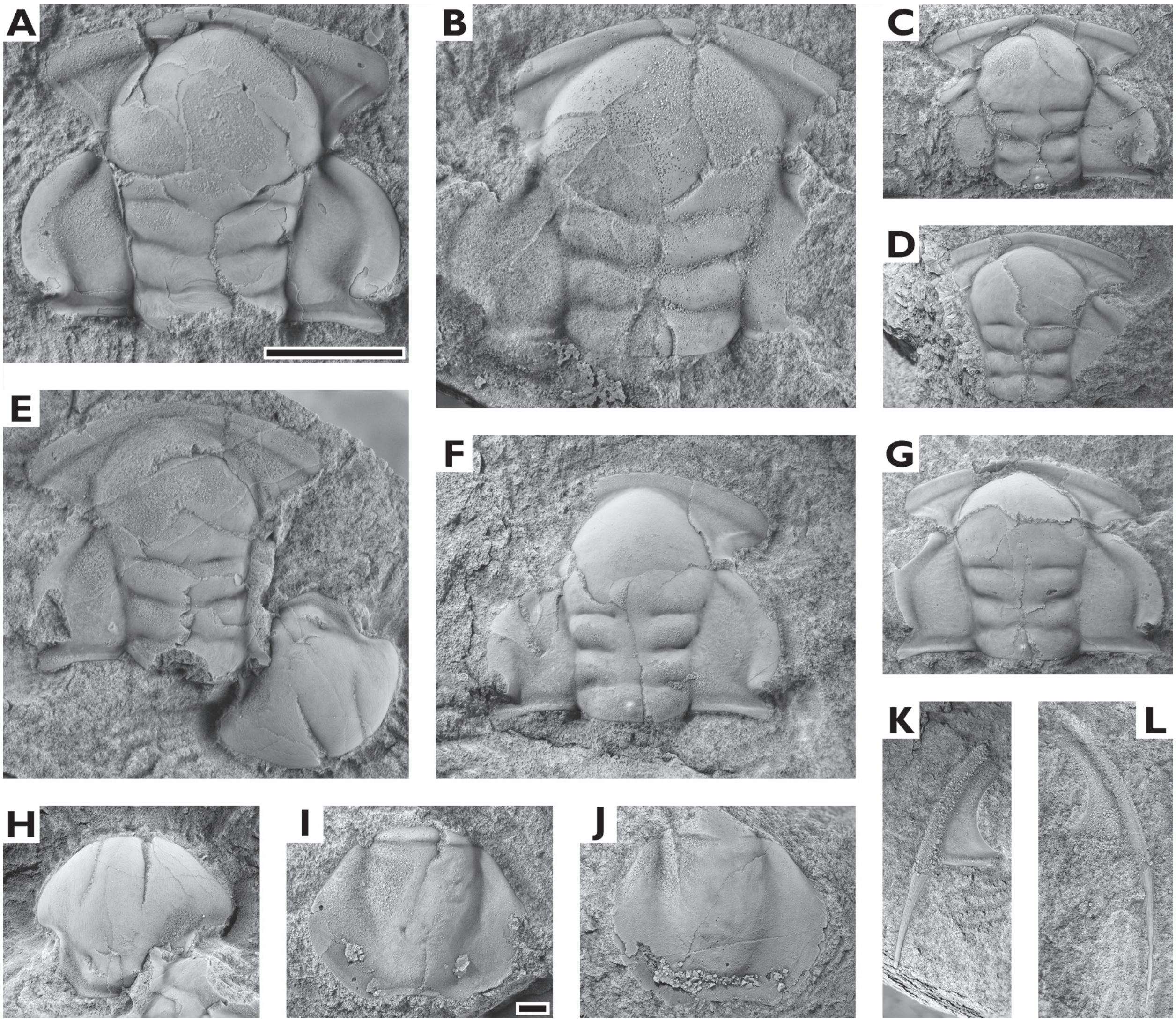


Fig. 48. ***Acadoparadoxides* (*Acadoparadoxides*) *torelli* (Westergård *in* Asklund & Thorslund, 1935)**, *A. pinus* – *P. praecurrens* Zone. **A–G**, cranidia. PMU 23034, 23039, 23045, 23041, 23037/3, 23036, 23040. **H**, hypostome. PMU 23037/4. **I–J**, pygidia. PMU, 23042, 23038. **K–L**, librigenae. PMU 23037/1, 23037/2. A is from Stendalsbäcken, B–L are from Björnbäcken. Scale bar for cranidia and librigenae = 10 mm, for pygidia = 1 mm.

On the Tåsjö Mountain, *A.* (*A.*) *torelli* was collected at Kvarnbäcken, Rökbergsbäcken and Marbäcken, at the latter two localities co-occurring with *P. praecurrens*. Elsewhere in Sweden, the species is reported from the *A. pinus* – *P. praecurrens* Zone in central Jämtland (Thorslund 1949), Östergötland and Öland (Westergård 1953). It has been listed also from Norway (Strand 1929) and Poland (Żylińska & Szczepanik 2009).

Remarks. – In contrast to the contemporaneous faunas described from central Jämtland and Öland, and even from the Tåsjö Mountain, the fauna of the *A. pinus* – *P. praecurrens* Zone is in Västerbotten of extremely low diversity. The only associated agnostoid is *P. praecurrens*, but rare brachiopods and hyoliths were also collected at Björnbäcken, where the zone is exposed for quite some distance in the river and contains common limestone concretions (Mannelqvist 2016). For a comprehensive description of *A. torelli*, based on material from the Tåsjö Mountain and the lectotype from Öland, see Weidner *et al.* (2014). These authors also remarked on the differences from other species of *Acadoparadoxides*.

Subgenus *Acadoparadoxides* (*Baltoparadoxides*) Šnajdr, 1986

Type species (OD). – *Paradoxides oelandicus* Sjögren, 1872, from the '*Paradoxides oelandicus* Beds' (Bårstad Mbr, Borgholm Formation) at Stora Frö [or Borgholm], Öland, Sweden.

Diagnosis. – See Dean & Rushton (1997).

Remarks. – Three species of *Acadoparadoxides* (*Baltoparadoxides*) are described from the Miaolingian of Scandinavia, viz. *A.* (*B.*) *oelandicus* (Sjögren, 1872), *A.* (*B.*) *bidentatus* (Westergård, 1936) and *A.* (*B.*) *quadrimucronatus* (Westergård, 1936).

Acadoparadoxides (*Baltoparadoxides*) *oelandicus* (Sjögren, 1872)

1872 *Paradoxides Oelandicus* sp. n. Sjögren, p. 72, pl. 5, fig. 1.
1877 *Paradoxides ölandicus* Sjögren; Linnarsson, p. 354, pl. 14, figs 1–6.
1882a *Paradoxides Ölandicus* Sjögren; Brøgger, p. 146.
1885 *Paradoxides oelandicus* Sjögren; Roemer, p. 24, pl. 1, fig. 3.
1929 *Paradoxides ölandicus* Sjögren; Strand, p. 350.
1936 *Paradoxides oelandicus* Sjögren; Westergård, pp. 33, 51, pl. 2, figs 1–11; pl. 3, figs 1–6; textfig. 8.
1952 *Paradoxides ölandicus* Sjögren; Henningsmoen, p. 16, pl. 1, fig. 1.
1957 *Eccaparadoxides oelandicus* (Sjögren); Šnajdr, p. 238.
1958 *Eccaparadoxides*? *oelandicus* (Sjögren); Šnajdr, p. 115.
1967 *Paradoxides ölandicus* Sjögren; Hucke & Voigt, p. 49, pl. 5, figs 2, 3.
1970 *Paradoxides oelandicus* Sjörgen [*sic*]; Bednarczyk, p. 34, pl. 1, fig. 1.
1979 *Paradoxides oelandicus* Sjögren; Neben & Krueger, p. 3, pl. 115, fig. 15; pl. 116, figs 1–5, 7–8.
1986 *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* (Sjögren); Šnajdr, p. 174 [*Baltoparadoxides* erected].
1989 *Eccaparadoxides oelandicus* (Sjögren); Ahlberg, p. 146, fig. 8.
1990 *Eccaparadoxides oelandicus* (Sjögren); Bednarczyk, Lendzion & Orlowski *in* Pajchlowa, p. 61, pl. 16, fig. 10.
pars 1994 *Eccaparadoxides oelandicus* (Sjögren); Rudolph, p. 169, pl. 16, figs 1–4, 6–9; *non* fig. 5 [= indet.].
1997 *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* (Sjögren); Dean & Rushton, p. 474, fig. 305:1a, b.
2007 *Paradoxides* (*Acadoparadoxides*) *oelandicus* Sjögren; Żylińska & Masiak, p. 681 (*cum syn.*, these have not been checked by us), fig. 11a–c, e, f, h, i.
2009 *Paradoxides* (*Acadoparadoxides*) *oelandicus* (Sjögren); Żylińska *in* Żylińska & Szczepanik, pl. 4, fig. 7.
2014 *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* (Sjögren); Weidner, Rushton & Ebbestad, p. 523, fig. 12C?, D?, E–F.

Holotype. – Incomplete thorax, NRM Ar1449, from the '*Paradoxides oelandicus* Beds' (Bårstad Mbr, Borgholm Formation) at Stora Frö [or Borgholm], Öland, Sweden. It was illustrated by Sjögren (1872, pl. 5, fig. 1) and refigured by Linnarsson (1877, pl. 1, fig. 5) and Westergård (1936, pl. 2, fig. 10).

Material and occurrence. – From the Lower Allochthon only the few specimens described by Weidner *et al.* (2014) from the Tåsjö Mountain in Ångermanland are known. The *A.* (*B.*) *oelandicus* Superzone was encountered at Stendalsbäcken, Björnbäcken and Storvindeln without finding the eponymous trilobite. Elsewhere in Sweden, *A.* (*B.*) *oelandicus* is common on Öland, in Östergötland, Närke and the autochthon of Jämtland (Westergård 1936, 1953; Rushton & Weidner 2007; collection TW, the latter material is stored at PMU). It ranges through the *E. insularis* and *A. pinus* – *P. praecurrens* zones, but is most numerous in the upper part of the older zone (Westergård 1936), which so far has been recognized with certainty only on Öland and below Gotland (for remarks on reports of the *E. insularis* Zone in Jämtland, see section on Biostratigraphy). The species is reported also from the *A. pinus* – *P. praecurrens* Zone at various localities in Norway (Brøgger 1882a; Strand 1929; Henningsmoen 1952). In the Holy Cross Mountains in Poland, it occurs in both zones (Żylińska & Masiak 2007). The only report from outside Baltica is from western Mongolia (Tomczykowa *in* Dumicz, Tomczykowa & Wójcik 1970). The Mongolian material may in part belong to the species, but a pygidium that unambiguously can identify the species was not illustrated. The figured thorax (*ibid*. pl. 13, fig. 9) shows pleurae extending straight out and then abruptly bending backwards, while the pleurae in *Acadoparadoxides* (*B.*) *oelandicus* are evenly curved outwards and backwards, sabre-like.

Remarks. – Several complete specimens of *A.* (*B.*) *oelandicus* and *A.* (*A.*) *pinus* have been described from Scandinavia whereas only pygidia of *bidentatus* and *quatrimucronatus* are known. The four taxa can be distinguished by their pygidia (Westergård 1936). Otherwise, in order to determine paradoxidid species, frequently even genera, a complete cranidium in addition to the pygidium and preferably a complete dorsal shield is required (Geyer 1993; Weidner *et al*. 2014).

Acadoparadoxides **sp.**

Figure 49A–D

Material and occurrence. – Two cranidia, both longitudinally compressed, one fragmentary cranidium, laterally compressed, and one pleural lobe of a thoracic segment were collected from the *A. pinus* – *P. praecurrens* Zone at Hemfjäll. They occur associated with *Pentagnostus praecurrens*.

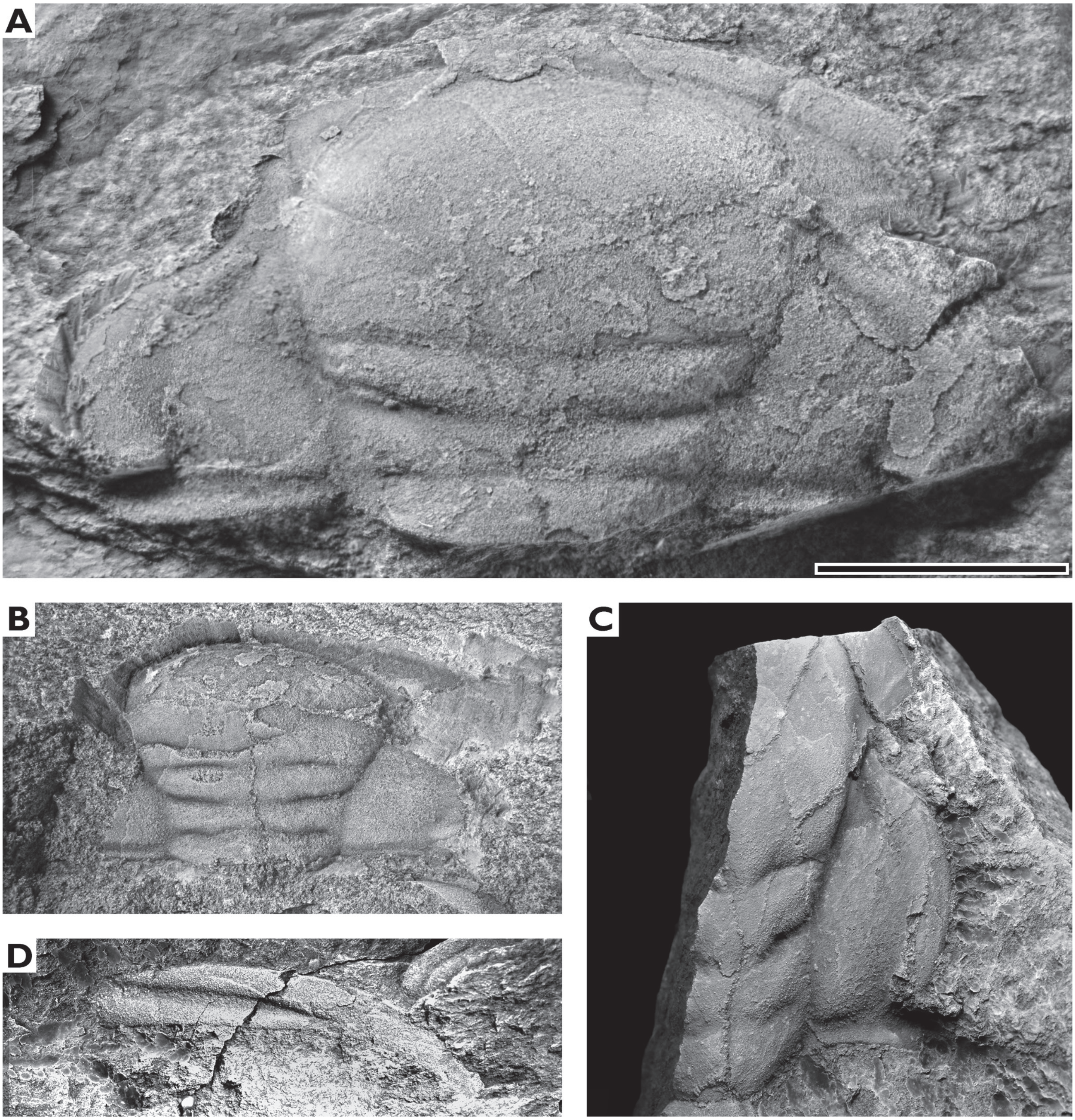


Fig. 49. ***Acadoparadoxides*** **sp.**, *A. pinus* – *P. praecurrens* Zone, Hemfjäll. **A–C**, cranidia. PMU 31643, 31639, 37222. **D**, a right pleura. PMU 37221. Scale bar = 10 mm.

Remarks. – The larger cranidium (Fig. 49A) shows an anterior border all along the cranidial front, narrowing medially. A preglabellar field is not developed. The glabella expands forwards; two pairs of glabellar furrows are connected across the glabella, but shallow medially. The palpebral lobes are long, strongly curved, and they become broader (tr.) rearwards and almost reach the posterior border. These features are typical for *Acadoparadoxides* and the larger specimen can best be compared to *Acadoparadoxides* (*s.l.*) spp. from the Tåsjö Mountain illustrated by Weidner *et al.* (2014, fig. 12C). The second cranidium (Fig. 49B), probably a small holaspid, is tentatively assigned to the same genus. The pleura is evenly curved outwards and backwards, as in *Acadoparadoxides* and differs in this feature from *Hydrocephalus* and *Eccaparadoxides* that occur in the same zone (Fig. 49D).

Genus *Hydrocephalus* Barrande, 1846

Type species (SD, Šnajdr, 1958). – Hydrocephalus carens, Barrande, 1846, from the *Eccaparadoxides pusillus* Zone at Týřovice, Bohemia, Czechia.

Diagnosis. – See Šnajdr (1987), Dean & Rushton (1997) and Fletcher *et al.* (2005).

Remarks. – Fletcher *et al.* (2005) ranked *Hydrocephalus* as a subgenus of *Paradoxides*, which is not followed here (see comments on genus by Rushton & Weidner 2007). Two species, *H. vikensis* Rushton & Weidner, 2007 and *H. spinulosus* Rushton *et al.*, 2016, are described from the Miaolingian of Scandinavia.

Hydrocephalus vikensis Rushton & Weidner, 2007

?1936 *Paradoxides* sp. No. 4 Westergård, pl. 7, fig. 13.
pars 2007 *Hydrocephalus vikensis* sp. nov. Rushton & Weidner, p. 396, pl. 1, figs 11–15; pl. 2, figs 1, 3–8; pl. 3, figs 1?, 2?, 3–5, 8–19; *non* pl. 3, figs 6, 7? [= *H. spinulosus* Rushton *et al.*, 2016].
2007 *Hydrocephalus* n. sp. (Typ 1) Münder, sp. 144, fig. 2.
2011 *Hydrocephalus vikensis* Rushton & Weidner; Weidner & Ebbestad, sp. 73, fig. 1.
2014 *Hydrocephalus vikensis* Rushton & Weidner; Weidner, Rushton & Ebbestad, p. 525, fig. 13A, B, C?, D?, E?
2016 *Hydrocephalus vikensis* Rushton & Weidner; Rushton, Weidner & Ebbestad, p. 548, figs 20B; 29B, D–E, G; 30B–D; 31B.

Holotype. – NRM Ar60130, a slightly distorted axial shield about 60 mm long figured by Rushton & Weidner (2007, pl. 1, fig. 11, 14; pl. 2, fig. 4), from the *A. pinus* – *P. praecurrens* Zone at Viken, Näkten, Jämtland, Sweden.

Remarks. – *Hydrocephalus vikensis* was originally described from autochthonous strata in Jämtland (Rushton & Weidner 2007) and subsequently recorded also at two localities in the Lower Allochthon on the Tåsjö Mountain (Weidner *et al.* 2014). Everywhere it occurs in the *A. pinus* – *P. praecurrens* Zone. Further north, no additional finds were made during this study. In Jämtland, *H. vikensis* occurs associated with *H. spinulosus* Rushton *et al.*, 2016 and for description of both species we refer to Rushton *et al.* (2016). The two species are primarily distinguished by the shape of the thoracic pleurae.

Genus *Paradoxides* Brongniart, 1822

Type species (SD, Barrande, 1852). – Entomostracites paradoxissimus Wahlenberg, 1818, probably from the *T. gibbus* Zone, Alum Shale Formation, Oltorp, Västergötland, Sweden. [ICZN 1957, Opinion 496].

Diagnosis. – See Dean & Rushton (1997).

Remarks. – Four species, *P. paradoxissimus* (Wahlenberg, 1818), *P. forchhammeri* Angelin, 1851, *P. davidis* Salter, 1863 and *P. jemtlandicus* Wiman, 1903 are described from the Miaolingian of Scandinavia.

Paradoxides forchhammeri Angelin, 1851

Figure 50A–P

1851 *Paradoxides forchhammeri* n. sp. Angelin, p. 2, pl. 2, figs 1–3.
1878 *Paradoxides forchhammeri*, Angelin; Brøgger, p. 37, pl. 1; pl. 2, figs 7–10.
1902 *Paradoxides forchhammeri* Angelin; Grönwall, p. 112.
1929 *Paradoxides forchhammeri* Angelin; Strand, p. 350.
1953 *Paradoxides forchhammeri* Angelin; Westergård, p. 36.
1978 *Paradoxides forchhammeri* Angelin; Bergström & Levi-Setti, p. fig. 7d; pl. 8, figs 2, 5–6.
1982 *Paradoxides* aff. *forchhammeri*; Kulling, p. 63.
2000 *Paradoxides forchhammeri* Angelin; Hammer, p. 251, figs 1, 2, 4, 5, 15, 16.

Type material. – *Paradoxides forchhammeri* was figured firstly without description based on material collected at Andrarum, Scania (Angelin 1851). Brøgger (1878), studying material from Krekling, Norway, treated the species in more detail, while Bergström & Levi-Setti (1978) briefly commented the species, but none referred to Angelin`s type material which probably is lost.

Material and occurrence. – Most of our new material is from the lower part of the *L. laevigata* Zone at Abborrfallet in northern Jämtland, where the richest fauna of the Miaolingian in our study area has been found. Additional material derives from Brattbäcken on the Tåsjö Mountain and Stendalsbäcken in the Vilhelmina area, where *P. forchhammeri* occurs

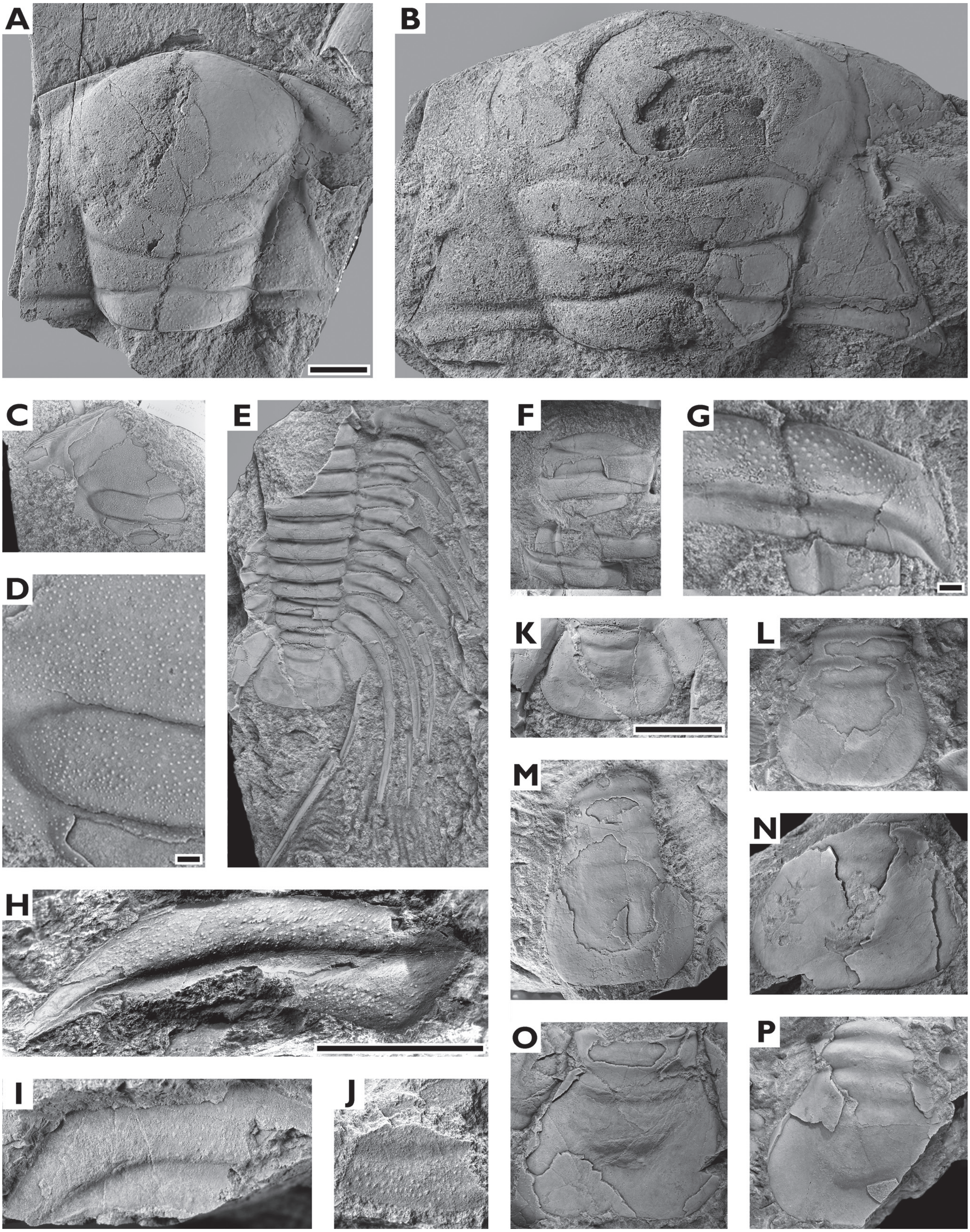


Fig. 50. ***Paradoxides forchhammeri* Angelin, 1851**, from the *P. forchhammeri* Superzone. The material from Brattbäcken and Stendalsbäcken are from the *G. nathorsti* Zone, and the material from Abborrfallet is from the lower part of the *L. laevigta* Zone. At Viejenäs, the zonation is unknown. **A–B**, cranidia from Abborrfallet. SGU 9912, 9913. **C**, cranidium, **D**, close-up view of the M2 glabellar lobe showing the coarse surface granulation, **E**, part of the thorax with the hindmost 11 pleurae and **K**, the pygidium, all of the same specimen from Brattbäcken. PMU 26288, 26289. **F–G**, axial rings, G as a close-up view showing the coarse surface granulation, also from Brattbäcken. PMU 26290. **H–J**, pleural fragments. H from Stendalsbäcken. I–J from Viejenäs. PMU 37224, 37225/1, 37226. **K–P**, pygidia. K from Brattbäcken, PMU 26289. L–O from Abborrfallet, SGU 9896, 9911, 9907, 9897. P from Abborrfallet, PMU 26591/2. Scale bar = 10 mm for A–C, E–F, scale bar = 1 mm for D and G, scale = 10 mm for H–J, and scale bar = 10 mm for K–P.

associated with *G. nathorsti*, *T. exsculpta*, *A. ferox*, *D. planicauda bilobatus* and *V. marginatus* in the *G. nathorsti* Zone. Except for Abborrfallet, *P. forchhammeri* occurs only sporadically in the studied sections. Asklund & Thorslund (1935) reported the species from Sågbäcken and *P.* cf. *forchhammeri* from Fånån, Karbäcken and Kvarnbäcken. From Viejenäs in Norbotten only fragments have been collected (see also Kulling 1982). Elsewhere in Sweden, *P. forchhammeri* is reported from the lower part of the *L. laevigata* Zone in Scania, Öland, Västergötland and Östergötland (Westergård 1953). Grönwall (1902) noted occurrence in the Andrarum Limestone on Bornholm, Denmark, and Brøgger (1878) described the species from Krekling, apparently from the upper part of the *G. nathorsti* Zone, and from Breidengen in Norway.

Paradoxides forchhammeri is known only from Scandinavia. The eponymous superzone comprises the *G. nathorsti*, *L. laevigata* and *A. pisiformis* zones, but *P. forchhammeri* seemingly appears somewhere in the *G. nathorsti* Zone and probably close to the top of it. The species is best known from the lower part of the *L. laevigata* Zone, but it may extend into the upper part of this zone (Grönwall 1902; Westergård 1953). Hence, it is an approximation to define the *P. paradoxissimus/P. forchhammeri* superzone boundary at the base of the *G. nathorsti* Zone, hinging on the LAD of *P. paradoxissimus* in the *P. punctuosus* Zone (Fig. 2).

Remarks. – Although recorded in most Swedish provinces with Cambrian strata, *P. forchhammeri* is comparatively poorly known as descriptions and illustrations are very scarce due to the lack of well-preserved material. In fact, no complete specimen is known. Angelin (1851) published a drawing of a complete specimen showing 17 segments, but this number seems doubtful (Bergström & Levi-Setti 1978).

Brøgger (1878) described some features of the cranidium, the librigenae, the hypostome and the pygidium, which were illustrated by a few drawings (*ibid.* pl. 1; pl. 2, figs 7–10). Laterally from the midpoint of the anterior border is on both sides a weak indentation, which is reflected also on the glabella (*ibid.* pl. 1); this feature is apparently not developed in specimens from Sweden (cf. Brøgger 1878). The glabella has two furrows (S1 and S2) which extend across it and two furrows (S3 and S4) which extend about halfway to the glabellar midline. In the pygidia, a short and wide form and a long and narrow form are distinguished (see also Grönwall 1902). The pygidial axis has 4-5 axial rings and the posterior border is indented. Occasionally minute lateral spines can be observed in both forms, located where the pygidium is widest. The complete carapace is covered with coarse granules. *Paradoxides forchhammeri* is one of the largest Cambrian trilobites occurring in Scandinavia, attaining a maximum length estimated at around 30 cm.

Strand (1929) mentioned as diagnostic characters the short palpebral lobes and the coarse surface granulation.

In their discussion of *P. davidis* and its subspecies, Bergström & Levi-Setti (1978) remarked on *P. forchhammeri* and figured a cranidium, two pygidia and a reconstruction of a complete specimen based on fragmentary material and drawings, most notably from Brøgger (1878). The number of thoracic segments remains uncertain. *Paradoxides forchhammeri* has four glabellar furrows; S1 and S2 are transglabellar while S3 and S4 do not extend to the glabellar midline and this is the primary difference from *P. davidis* subspecies, which lack the latter two. The trapezoidal shape of the pygidium in *P. davidis trapezopyge*, considered as a close forerunner of *P. forchhammeri* by Bergström & Levi-Setti (1978), and the comparatively coarse granulation in *P. davidis brevispinus* are traits shared with *P. forchhammeri*.

In two cranidia collected by Westergård at Abborrfallet and housed in the SGU-collection (here illustrated in Fig. 50A–B), a very faint S3 furrow can be discerned only in the larger specimen (when studied under strong magnification). In a cranidium from Brattbäcken (Fig. 50C), both S3 and S4 furrows are visible. The illustrated pygidia represent the short and wide form (Fig. 50K–P). They differ from the specimen illustrated by Brøgger (1878, pl. 2, fig. 7) and also from the pygidia of *P. davidis trapezopyge* in that the posterior border is straight and lacks a distinct indentation. Two pygidia illustrated in Fig. 50K–L reveal under strong magnification the minute lateral spines mentioned by Brøgger (1878). The better preserved material from Brattbäcken shows the dense and coarse granulation (Fig. 50D, G). Kulling (1982, p. 63) reported granulated fragments of '*Paradoxides*' from a locality in the Gautojaure Window in Norrbotten. We rediscovered the outcrop at Viejenäs, which yielded thoracic fragments with distinct coarse granulation (Fig. 50I, J).

Paradoxides paradoxissimus (Wahlenberg, 1818)

Figures 51, 52, 53

1818 *Entomostracites paradoxissimus* Wahlenberg, p. 34, pl. 1, fig. 1.
1878 *Paradoxides tessini* Brongniart; Brøgger, p. 43, pl. 2, fig. 6; pl. 4, fig. 9.
1879 *Paradoxides Tessini* Brongniart; Linnarsson, p. 6, pl. 1, figs 1–4.

1883 *Paradoxides tessini* Brongniart; Linnarsson, p. 10, pl. 1, figs 1–13.
pars 1994 *Paradoxides paradoxissimus* (Wahlenberg); Rudolph, p. 166, pl. 14, figs 1–5, 7–12; *non* pl. 14, fig. 6 [= *Paradoxides jemtlandicus*? Wiman, 1903].
2009 *Paradoxides paradoxissimus* (Wahlenberg); Weidner & Nielsen, p. 266, fig. 16A–D.
2014 *Paradoxides paradoxissimus* (Wahlenberg); Weidner & Nielsen, p. 79 (*cum syn.*), fig. 47A–G.

Lectotype (designated by C. Poulsen 1956). – Complete specimen, NRM Ar46147, illustrated by Westergård (1953, pl. 8, fig. 2) and refigured by Levi-Setti (1993, pl. 82) and Dean & Rushton (1997, fig. 304:1a). It probably originates from the *T. gibbus* Zone in the Alum Shale Formation at Oltorp, Falbygden, Västergötland, Sweden.

Material and occurrence. – Cranidia, hypostomes, pleurae and pygidia of *P. paradoxissimus* are common in the *A. atavus* Zone at Karbäcken, Bellviks Hällan, Djupdalsbäcken, Stendalsbäcken and Fjällbränna. Unusually large cranidia, up to five cm long, were collected from a few cm thick *P. paradoxissimus*-fragment limestone bed in the *A. atavus* Zone at Stendalsbäcken (Fig. 51). At Stendalsbäcken and Granberget as well as at Kvarnbäcken on the Tåsjö Mountain, *P. paradoxissimus* occurs also in the *P. punctuosus* Zone associated with *D. incertus*, *L. elegans* and *L. lundgreni*. Smaller fragments, likely belonging to the species, have been reported also from the *A. atavus* Zone at various localities on the Tåsjö Mountain (Asklund & Thorslund 1935). *Paradoxides paradoxissimus* is known from many localities throughout Scandinavia and ranges through the *T. gibbus*, *A. atavus* and *P. punctuosus* zones (Grönwall 1902; Westergård 1953; Rudolph 1994). *Paradoxides paradoxissimus* is restricted to Scandinavia but the Bohemian *Paradoxides gracilis* (Boeck, 1828) is a close relative.

Remarks. – Complete specimens of *P. paradoxissimus* are rare but disarticulated cranidia, thoracic pleurae and pygidia are very common. The glabella is club-shaped and widens evenly forwards, slightly pointed sagitally; its maximum width is about 1½ times the width at the glabellar base. In the large cranidia from Stendalsbäcken, the glabella expands evenly towards the S2-furrows, then widens more strongly forwards. The border furrow narrows medially. Two pairs of glabellar furrows curve slightly backwards and traverse the glabella; S3 is faintly impressed laterally. The palpebral lobes are of medium length.

The pygidium of *P. paradoxissimus* is longer than wide and subquadrate to subpentagonal and the axis shows three to four rings in addition to a terminal

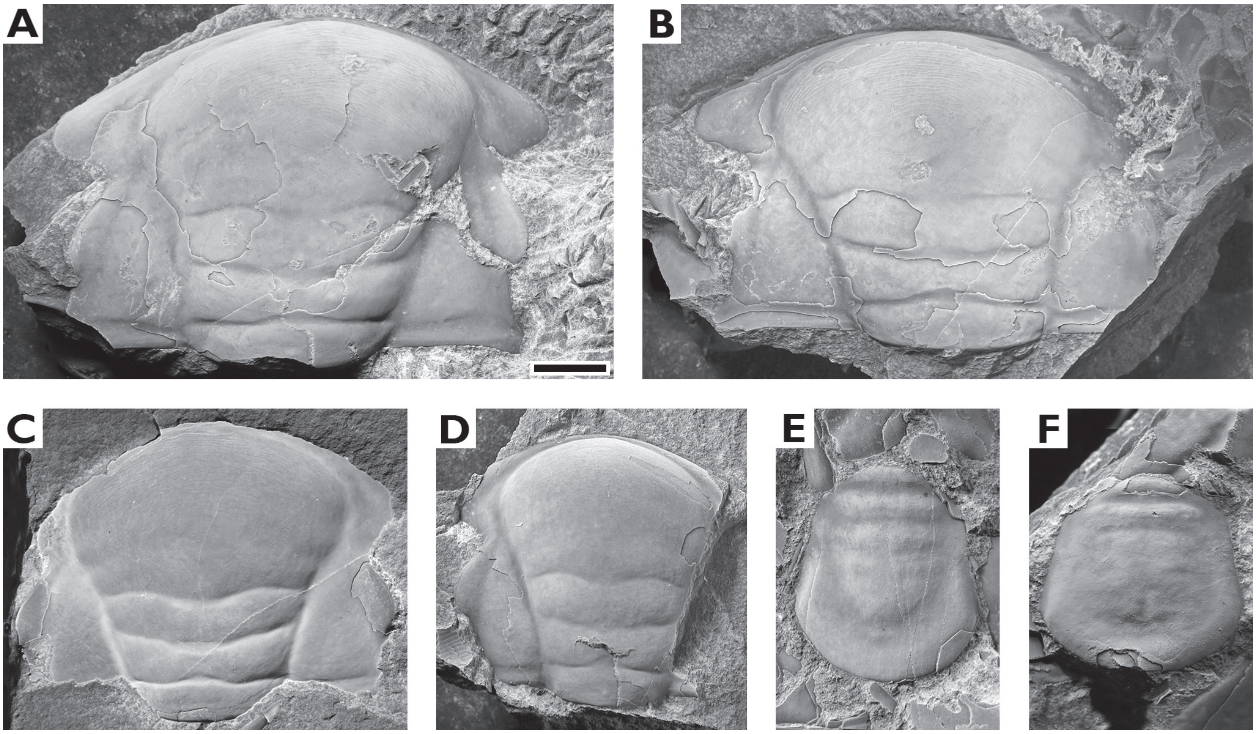


Fig. 51. ***Paradoxides paradoxissimus* (Wahlenberg, 1818)**, unusually large specimens from the *A. atavus* Zone at Stendalsbäcken. **A–D**, cranidia. PMU 36429, 36428, 39154, 39153, **E–F**, pygidia. PMU 36430, 36431. Scale bar = 10 mm.

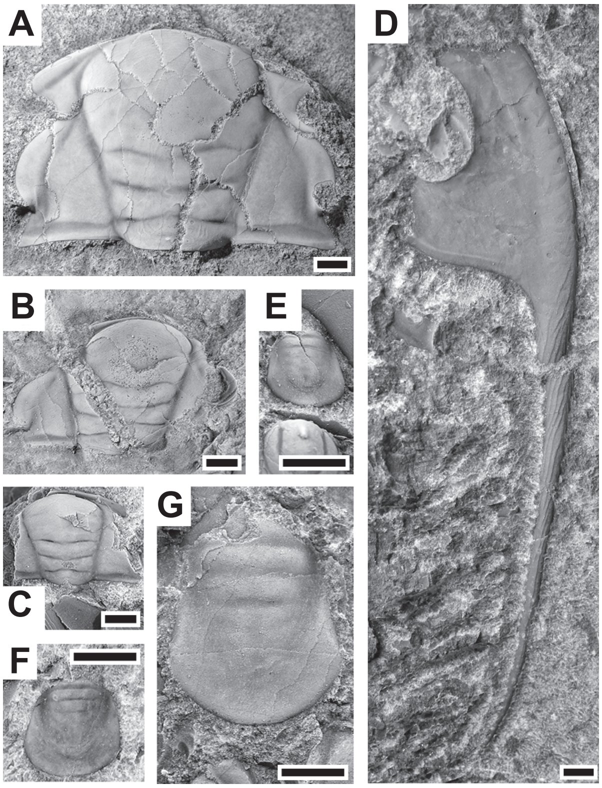


Fig. 52. ***Paradoxides paradoxissimus*** **(Wahlenberg, 1818)**, from the *A. atavus* Zone. **A–C**, cranidia. PMU 26174, 26177b/4, 37192/2. **D**, right librigena. PMU 37161/4. **E–G**, pygidia. PMU 37193/2, 37188/4, 37223. A–B are from Bellviks Hällan, C–G are from Djupdalsbäcken. Scale bars A–D = 2 mm, E–G = 2 mm.

piece. For detailed descriptions of the species, we refer the reader to Linnarsson (1879, 1883).

Both cranidia and pygidia are readily separated from *Mawddachites hicksii* (Salter, 1866) (see Lake 1935, p. 199; Fletcher 2007, pl. 8A–F) occurring in the *A. atavus* Zone, and from '*Paradoxides*' (*s.l.*) *palpebrosus* Linnarsson, 1879 (see Rudolph 1994, pl. 18, figs 1–9) from the *T. gibbus* Zone. Both those species occur associated with *P. paradoxissimus* on Bornholm, Denmark, and in Scania, Sweden, but they have not been found at other localities in Scandinavia (Westergård 1953; Weidner & Nielsen 2014). *Paradoxides paradoxissimus* resembles *P. davidis* Salter, 1863, from the *P. punctuosus* Zone, but in that species, the S1 and S2 furrows are directed more strongly backwards and the palpebral lobes are shorter. The pygidium of *P. paradoxissimus* is variable (Figs 51 & 53; Weidner & Nielsen 2009, 2014) as in *P. davidis*, but in that species the posterior border is straight with a small indentation (see Bergström & Levi-Setti 1978; Fletcher 2007, pl. 8.G–I) while in *P. paradoxissimus* the posterior border is always rounded.

One pygidium of *P. paradoxissimus* from the *P. punctuosus* Zone is wider and appear less elongate than is usual in this species (Fig. 53N). The same observation was made by Grönwall (1902) in pygidia from 'younger strata' (*P. punctuosus* Zone) at Øleå on Bornholm, Denmark. In this feature, the pygidia approach those of *P. davidis* and *P. forchhammeri*, both of which have a short and wide form and a long and narrow form.

Family Solenopleuridae Angelin, 1854

Genus *Solenopleura* Angelin, 1854

Type species (SD, Walcott, 1884). – Calymene holometopa Angelin, 1851, from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone at Andrarum, Scania, Sweden.

Diagnosis. – See Westergård (1953) and C. Poulsen (1959b).

Remarks. – The status of this genus has been much debated; see Westergård (1953), Rudolph (1994), Geyer (1998), Rushton & Berg-Madsen (2002), Fletcher (2007) and Esteve (2015). Some researchers favour a restricted concept of the genus and assign several solenopleurid-like species to other genera (e.g. *Brunswickia* Howell, 1937; *Parasolenopleura* Westergård, 1953; *Jincella* Šnajdr, 1957; *Erratojincella* Rudolph, 1994; *Foveatella* Rudolph, 1994; *Gonzaloia* Geyer, 1998), whereas other authors adopt a broader definition of *Solenopleura*. Rushton & Berg-Madsen (2002), Fletcher (2007) and Esteve (2015) all emphasized the need for further study before agreement on diagnostic features separating these genera is within reach. Pending a revision of the species group, we recognize the type species *Solenopleura holometopa* (Angelin, 1851) and tentatively assign eight additional taxa from the Miaolingian of Scandinavia to *Solenopleura*?, viz. *S.*? *brachymetopa* (Angelin, 1851); *S.*? *canaliculata* (Angelin, 1851); *S.*? *parva* Linnarsson, 1879; *S.*? *bucculenta* Grönwall, 1902; *S.*? *nuntia* Grönwall, 1902; *S.*? *munsteri* Strand, 1929; *S.*? *conifrons* Westergård, 1953 and S.? *nigra* (Rudolph, 1994).

***Solenopleura*? *brachymetopa* (Angelin, 1851)**

Figure 54A–F

1851 *Calymene brachymetopa* n. sp. Angelin, p. 23, pl. 19, fig. 1.
1854 *Solenopleura brachymetopa* n. sp. Angelin, p. 27, pl. 19, fig. 1.
1878 *Solenopleura brachymetopa* Angelin var. *alutacea*; Brøgger, p. 51, pl. 3, fig. 8.
1902 *Solenopleura brachymetopa* Angelin; Grönwall, p. 153, pl. 4, figs 15, 22.

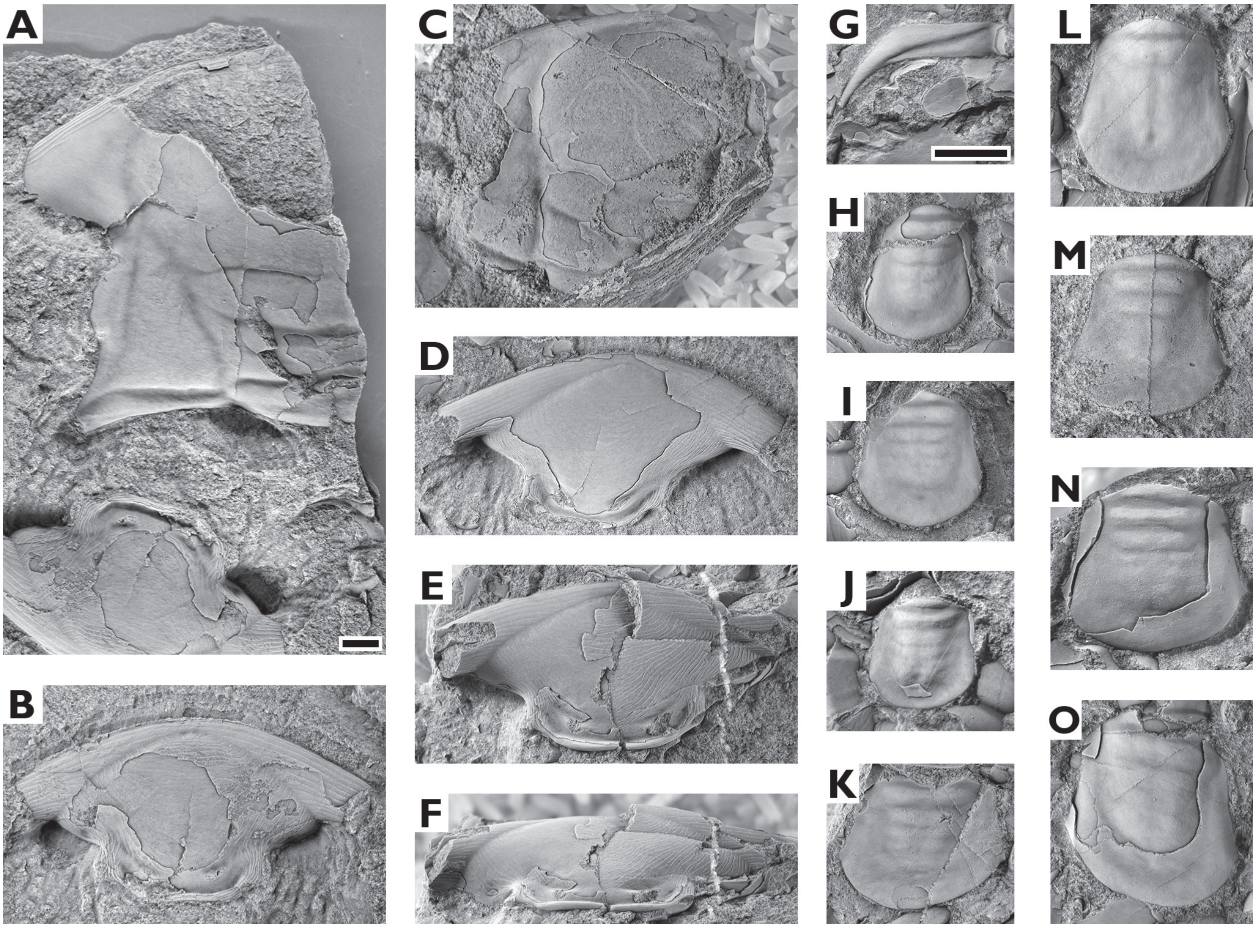


Fig. 53. ***Paradoxides paradoxissimus*** **(Wahlenberg, 1818)**, from the *P. punctuosus* Zone. **A, C,** cranidia, from Granberget. PMU 23083/2, 23081/2. **B**, hypostome, from Granberget. PMU 23083/1. **D**, **E–F**, two hypostomes from Stendalsbäcken, in dorsal and posterior view. PMU 23085/2, 23084. **G**, pleura, from Stendalsbäcken. PMU 23072/3. **H–O**, pygidia. PMU 23077, 23078/2, 23076/1, 23079, 23075, 23081/1, 23074, 23076/2. K and M are from Granberget, all others are from Stendalsbäcken. Scale bars A–F = 5 mm, G–O = 5 mm..

1953	*Solenopleura brachymetopa* (Angelin); Westergård, p. 18, pl. 3, figs 4–10.
1994	*Erratojincella brachymetopa* (Angelin); Rudolph, p. 206, pl. 25, figs 1, 2.

Lectotype (designated by Westergård 1953). – Cranidium, NRM Ar1773g, illustrated by Westergård (1953, pl. 3, fig. 4). The specimen is from the Andrarum Limestone Bed, lower part of the *L. laevigata* Zone, at Andrarum, Scania, Sweden.

Material and occurrence. – In the lower part of the *L. laevigata* Zone, one cranidium was found at Vedjeön, four at Abborrfallet and one at Fjällbränna. We also figure cranidia from Abborrfallet and Brattbäcken, kept in the SGU collection. The species has previously been reported from the same zone in northern Jämtland (Hillsand, Vedjeön, Siljeåsen, Abborrfallet) and the Tåsjö Mountain (Brattbäcken, Karbäcken) by Westergård (1953). Elsewhere in Sweden, *S.*? *brachymetopa* occurs in the Andrarum Limestone Bed and the coeval Exporrecta Conglomerate Bed (lower part of the *L. laevigata* Zone) in Scania, on Öland, and in Västergötland (Westergård 1953). It is known also from Norway (Brøgger 1878), Bornholm, Denmark (Grönwall 1902) and ice-rafted boulders found in Germany (Rudolph 1994) and at As Hoved, Denmark (collection TW). The species is generally common. It is known only from Scandinavia.

Remarks. – We assign the cranidia to *S.*? *brachymetopa* because the moderately tapering glabella is bounded by deep and wide axial furrows and three glabellar furrows are visible of which the anterior is faint and the preceding two distinct; the preglabellar field is longer (sagitally) than the anterior border and moderately depressed in front of the glabella; the border furrow is narrow and deep but shallows medially; the posterior

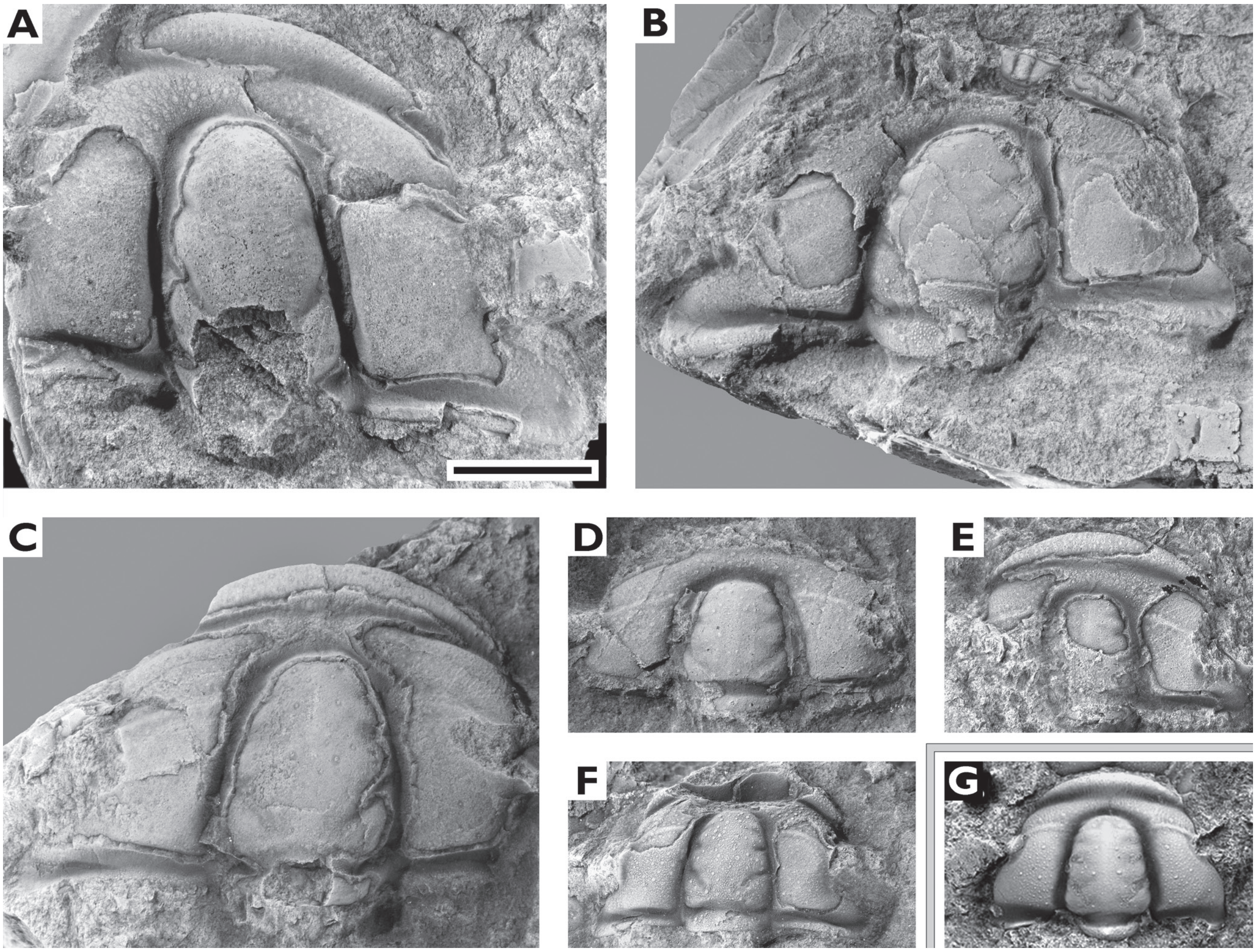


Fig. 54. ***Solenopleura? brachymetopa*** **(Angelin, 1851)**, **A–F**, cranidia from the lower part of the *L. laevigata* Zone. A is from Vedjeön. PMU 26140/1. B and C are from Abborrfallet. SGU 9908 and PMU 26583. D is from Brattbäcken. SGU 9901. E and F are from Abborrfallet. SGU 9905 and PMU 26584. ***Solenopleura? nuntia*** **(Grönwall, 1902)**. **G**, cranidium from the *A. atavus* Zone at Øleå, Bornholm, Denmark, shown for comparison. MGUH 30205. The specimen has been illustrated previously by Weidner & Nielsen (2014, fig. 51B). Scale bar = 5 mm.

parts of the fixigenae are wide (tr.) and the small palpebral lobes are situated at glabella midlength. Westergård (1953) described the glabella as being rather short and the palpebral lobes as small; in our specimens the glabella is relatively long due to tectonic distortion.

Solenopleura? *nuntia* Grönwall, 1902 from the *A. atavus* Zone of Bornholm was originally described as a variety of *S.*? *brachymetopa* (see Weidner & Nielsen 2014, p. 84, for description and remarks). It is distinguished by having a transverse narrower anterior border, a shorter preglabellar field (sag.), narrower interocular and posterior fixigenae (tr.), and the palpebral lobes are situated more anteriorly (Fig. 54G).

Genus *Parasolenopleura* Westergård, 1953

Type species (OD). – *Calymene aculeata* Angelin, 1851 from the Granulata Conglomerate Bed (Borgholm Formation), *T. gibbus* Zone at Borgholm, Öland, Sweden.

Diagnosis. – See Westergård (1953), C. Poulsen (1959) and Fletcher (2005).

Remarks. – See Rudolph (1994) and Geyer (1998) for discussion of genus. Five species are recorded from the Miaolingian of Scandinavia, viz. *P. aculeata* (Angelin, 1851), *P. cristata* (Linnarsson, 1877), *P. linnarssoni* (Brøgger, 1878), *P. scanica* Westergård, 1953, and *P. spinigera* Westergård, 1953. In addition, *P.*? *peregrina* (Wallerius, 1930) is questionable assigned. We consider *P. vestgothica* Westergård, 1953 as conspecific with *P. spinigera* (see remarks on *P. linnarssoni* below).

Parasolenopleura linnarssoni (Brøgger, 1878)

Figure 55A–D

1878 *Liostracus linnarssoni*, n. sp. Brøgger, p. 47, ?pl. 3, fig. 4a–c [= *P. linnarssoni* or *P. spinigera*; the diagnostic occipital ring is damaged].

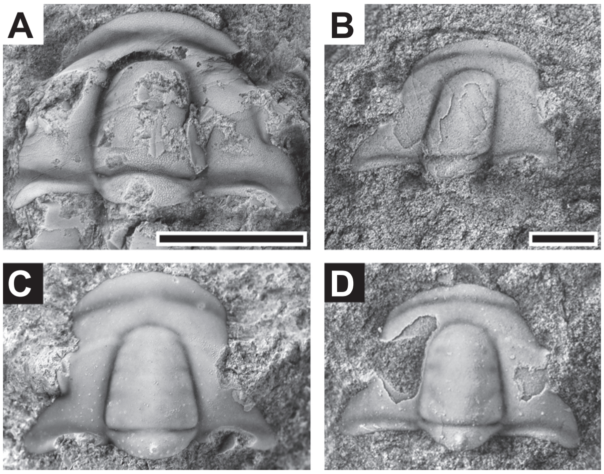


Fig. 55. ***Parasolenopleura linnarssoni*** **(Brøgger, 1878)**, *A. atavus* Zone. **A**, a larger cranidium from Karbäcken, PMU 26179, and **C**, a well-preserved cranidium of the same size from an ice-rafted boulder found at Sundsøre, Denmark, shown for comparison. MGUH 34047. **B**, a smaller cranidium from Högnäsån, PMU 26167, and **D**, a smaller undeformed cranidium from an ice-rafted boulder found at Barsø, Denmark, shown for comparison. MGUH 34048. Scale bar for A and C = 5 mm, for B and D = 1 mm.

non 1883 *Liostracus linnarssoni* Brögger; Linnarsson, p. 23, pl. 4 fig. 5 [= *Parasolenopleura spinigera* Westergård, 1953]; pl. 4, figs 6–9, 11 [= ?*Parasolenopleura* n. sp.]; pl. 4, fig. 10 [= indet.; a species of *Parasolenopleura*].
1902 *Liostracus linnarssoni* Brøgger; Grönwall, p. 144.
1929 *Liostracus linnarssoni* Brøgger; Strand, p. 351, pl. 1, fig. 19; pl. 2, fig. 6.
pars 1953 *Parasolenopleura linnarssoni* (Brögger) Westergård, p. 26, pl. 6, figs 9–10; *non* 11, 12 [= ?*Parasolenopleura* n. sp.]; ?pl. 7, figs 1–5 [= *P. linnarssoni* or *P. spinigera*].
1994 *Parasolenopleura linnarssoni* (Brögger); Rudolph, p. 214, pl. 26, figs 15, 16; pl. 27, figs 1–15.
2014 *Parasolenopleura linnarssoni* (Brøgger); Weidner & Nielsen, p. 85, fig. 52E–J.

Lectotype (designated by Westergård 1953). – Cranidium, PMO 19858, original of Brøgger (1878, pl. 3, fig. 4) and re-illustrated by Westergård (1953, pl. 7, fig. 1a–c). The lectotype derives from the *P. paradoxissimus* Superzone in the Alum Shale Formation at Krekling, Oslo Region, Norway.

Material and occurrence. – In the study area, *P. linnarssoni* was found in the *A. atavus* Zone only at Högnäsån and Karbäcken on the Tåsjö Mountain. Previously, it has been reported also from Abborrfallet (Asklund & Thorslund 1935), from Vedjeön and Sågbäcken (Westergård 1953) and from Lubbträsk (Kulling 1955). Elsewhere in Sweden, it has been recorded from Scania, Öland and Västergötland (Westergård 1953). It is known also from Bornholm, Denmark (Weidner & Nielsen 2014), Norway (Strand 1929), and ice-rafted boulders in Germany and Denmark (Rudolph 1994; collection TW). The species is most common in the *A. atavus* Zone, but in ice-rafted boulders and in Norway it also occurs in the *P. punctuosus* Zone (Rudolph 1994; personal communication Magne Høyberget 2016). The species is known only from Scandinavia.

Remarks. – Parasolenopleura linnarssoni, P. spinigera and *P. vestgothica* (the last regarded as a synonym of *P. spinigera*), constitute a closely related species group. *Parasolenopleura linnarssoni* has a node on the occipital ring whereas *P. spinigera* and *P. vestgothica* possess a spine, which is supposed to be more prominent in the latter (Westergård 1953). Investigation of extensive material from Sweden, Norway and Denmark (Bornholm), still unpublished (Weidner & Nielsen in prep.), shows that certain cranidial features of the three species vary considerably during ontogeny and often also among similarly sized specimens (see also Fletcher 2005). We conclude that there is one form with an occipital node (*P. linnarssoni*) and another with an occipital spine (*P. spinigera* as senior synonym). Linnarsson (1883) illustrated cranidia without a node nor a spine, and these may constitute a third species within in this group. We have not yet found corresponding material.

Parasolenopleura scanica occurs in the *T. gibbus* and *A. atavus* zones and can be distinguished from *P. linnarssoni* by the wider cranidium with a less arched anterior border and palpebral lobes that are situated more anteriorly.

Parasolenopleura aculeata from the *T. gibbus* Zone differs from *P. linnarssoni* in having a wider cranidium, a strongly upturned anterior border and an occipital spine.

Family Dorypygidae Kobayashi, 1935

Genus *Kootenia* Walcott, 1889

Type species (OD, Walcott, 1889). – Bathyuriscus (Kootenia) dawsoni Walcott, 1889, from the Burgess Shale of the Stephen Formation, British Columbia, Canada.

Diagnosis. – See C. Poulsen (1959a) and Palmer (1968).

Remarks. – Kootenia is a globally widespread and common genus in the lower Cambrian and Miaolingian with more than 100 species. In USA and Canada, it occurs in the Rocky Mountains, Appalachians, Great Basin, western Newfoundland and Alaska. Elsewhere, it is reported from Greenland, Scandinavia, U.K., Siberia, Kyrgyzstan, China, Korea, South America and Australia. From Scandinavia, only the very rare *K. westergaardi* Thorslund, 1949 has been described previously. It was found in the *A. pinus – P. praecurrens* Zone in the Lower Allochthon at Skute, near Brunflo, central Jämtland, Sweden (Thorslund 1949).

***Kootenia* sp.**

Figure 56A–F

Material and occurrence. – A single pygidium was found at Strömnäs associated with *H. lingula* and *H. truncatus*, which point to the *A. atavus* Zone.

Remarks. – The pygidium of *Kootenia* is characterized by a well-defined axis generally reaching to the inner edge of a moderately well-defined border. Three to five ring furrows are present. The pleural fields are crossed by three to five generally deep pleural furrows; interpleural furrows are barely visible or absent. The border has from four to seven pairs of spines, varying from mere scallops to long and stout spines, generally evenly spaced along the margin (C. Poulsen 1959; Palmer 1968).

At first glance the new pygidium seemed to be undeformed, but agnostoid shields from the sample were all tectonically distorted. Retro-deformation suggests that the pygidium was originally approximately 150% wider than immediately apparent (Fig. 56A versus 56B). The specimen is 15 mm long and has a well-defined, flat border, a slender, gently tapering axis, four non-spinose axial rings in addition to the terminal piece, ring furrows shallowing medially, four pleural furrows and at least four pairs of long and thick marginal spines.

Compared to *Kootenia* sp., the pygidium of *K. westergaardi* is much smaller and the largest specimen attains a lenght of only 5 mm. It differs further in having five axial rings, each one carrying an incipient spine or tubercle and the five pairs of marginal spines are short.

Closest resemblance of this specimen is to a pygidium of *K. sibirica* Lermontova, 1940, figured by Egorova *et al.* (1976, p. 86, pl. 29, fig. 15) and deriving from the Amgan Stage, Siberia. This Russian specimen has a slightly narrower border and indistinct nodes on the axial rings.

The restored form of the pygidium is also quite similar to pygidia of *Kootenia* reported from the Farewell Terrane in southwestern Alaska (see St. John & Babcock 1997, pp. 269–281). *Kootenia*? sp. (*ibid.* fig. 5R) is approximately 12 mm long, similar in shape, has four axial rings and a terminal piece, four pleural furrows and at least four pairs of marginal spines. It differs in having a narrower border, axial spines and shorter marginal spines. *Kootenia* n. sp. (*ibid.* fig. 5V) has the same number of axial rings, pleural furrows and marginal spines and is also of approximately the same size (17 mm). The main differences are the comparatively broader and parallel-sided axis with a

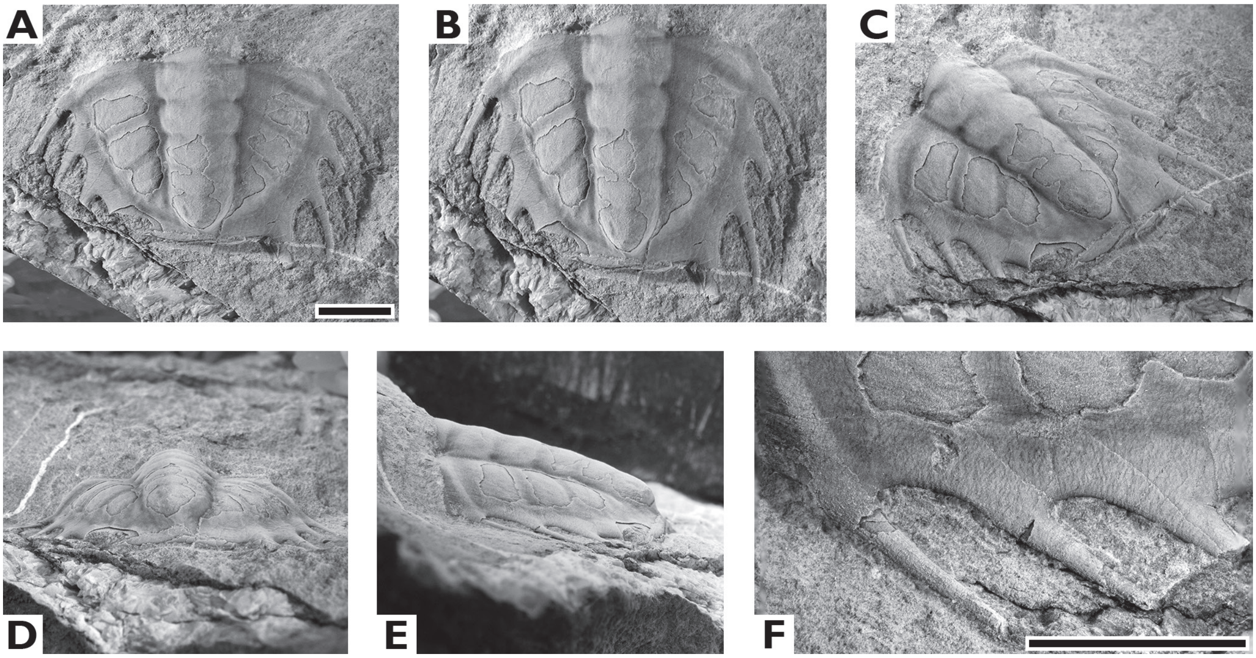


Fig. 56. ***Kootenia* sp.**, *A. atavus* Zone at Strömnäs. PMU 22839. **A**, retro-deformed pygidium shown in dorsal view. **B–E**, same pygidium in original shape, in dorsal, oblique, posterior and lateral views. **F**, close-up view of the spine base. Scale bars A–E = 5 mm, F = 5 mm.

terminal piece much longer (sag.) than the axial rings. Each of the axial rings and the terminal piece carry a faint node. The trilobite fauna of the Farewell Terrane shares with Siberia and Baltica a number of agnostoids and trilobites from the *P. punctuosus* Zone and lower part of the *L. laevigata* Zone.

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Appendix 1. Catalogue of the most important publications on the Miaolingian faunas of Scandinavia in the respective areas. See References for complete citations.

Bornholm

1902 Grönwall
1963 Poulsen, V.
1966 Poulsen, V.
1981 Berg-Madsen
1985a Berg-Madsen
1985b Berg-Madsen
1985c Berg-Madsen
1986 Berg-Madsen
2007 Weidner & Nielsen
2014 Weidner & Nielsen
2015a Weidner & Nielsen

Scania

1879 Linnarsson
1880 Tullberg
1883 Linnarsson
1942 Westergård
1944 Westergård
1946 Westergård
1948 Westergård
1950 Westergård
1953 Westergård
2003 Axheimer & Ahlberg
2007 Ahlberg *et al.*
2009 Laurie
2010 Dies Alvarez *et al.*
2015b Weidner & Nielsen
2016 Weidner & Nielsen
2018 Weidner & Ebbestad

Öland

1877 Linnarsson
1906 Wiman
1936 Westergård
1944 Westergård
2009 Weidner & Nielsen
2012 Buchholz

Bohuslän

1968 Martinsson

Västergötland

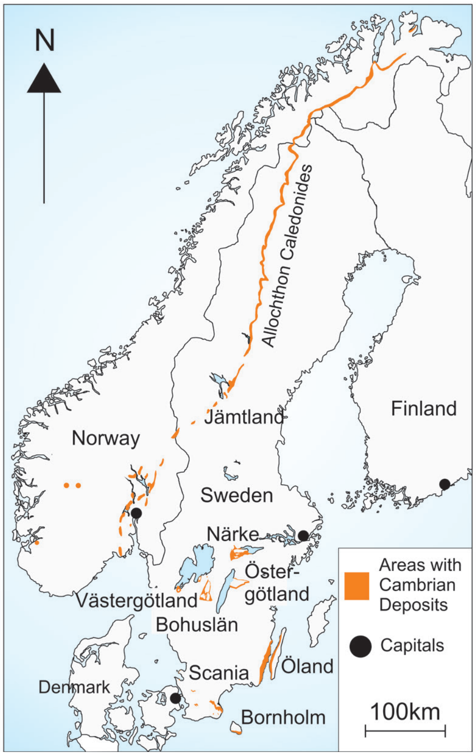
1869 Linnarsson
1873 Linnarsson
1877 Linnarsson
1894 Wallerius
1895 Wallerius
1896 Wallerius
1930 Wallerius
1944 Westergård
1946 Westergård
1948 Westergård
1950 Westergård
1953 Westergård
2004 Weidner *et al.*
2006 Axheimer *et al.*
2017 Ebbestad & Weidner

Central Jämtland

1903 Wiman
1940 Thorslund
1946 Westergård
1948 Westergård
1950 Westergård
1953 Westergård
1998 Karis
2006 Axheimer
2006 Rushton
2007 Rushton & Weidner
2013 Ebbestad *et al.*
2014 Weidner & Ebbestad
2016 Rushton *et al.*

Norway

1875 Brøgger
1876 Brøgger
1878 Brøgger
1882a Brøgger
1882b Brøgger
1902 Brøgger in Schiøtz
1929 Strand
1952 Henningsmoen
1984 Bruton *et al.*
1989 Bruton *et al.*
1990 Nikolaisen & Henningsmoen
1999 Bruton
2000 Hammer
2000 Bruton & Harper
2003 Ebbestad & Budd
2008 Høyberget & Bruton



Östergötland

1944 Westergård
1946 Westergård
1948 Westergård
1950 Westergård
1953 Westergård

Närke

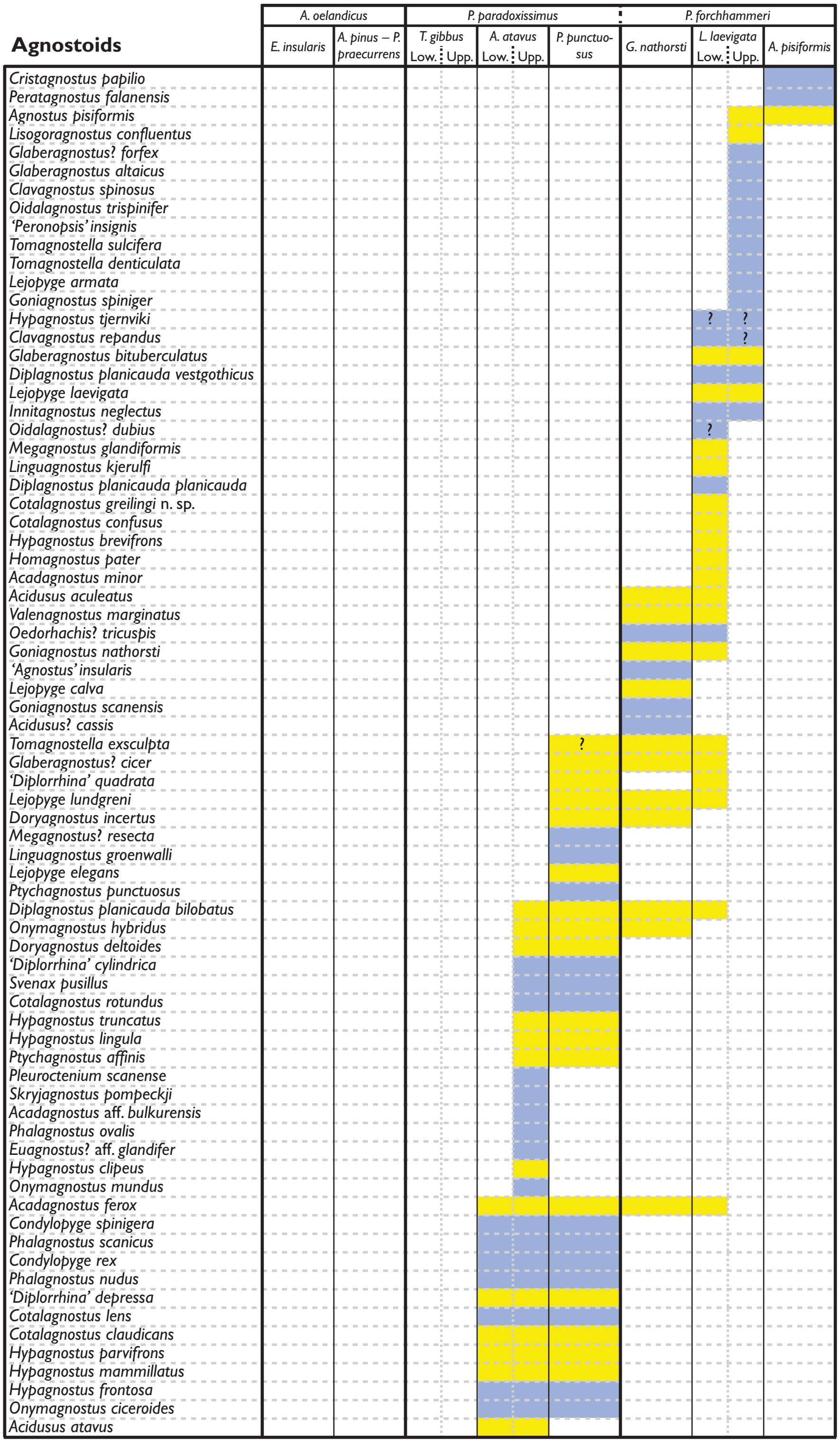
1946 Westergård
1948 Westergård
1950 Westergård
1953 Westergård

Allochthon Caledonides

1935 Asklund & Thorslund
1938 Asklund
1942 Kulling
1949 Thorslund
1955 Kulling
1998 Karis
2014 Weidner *et al.*
2016 Mannelqvist

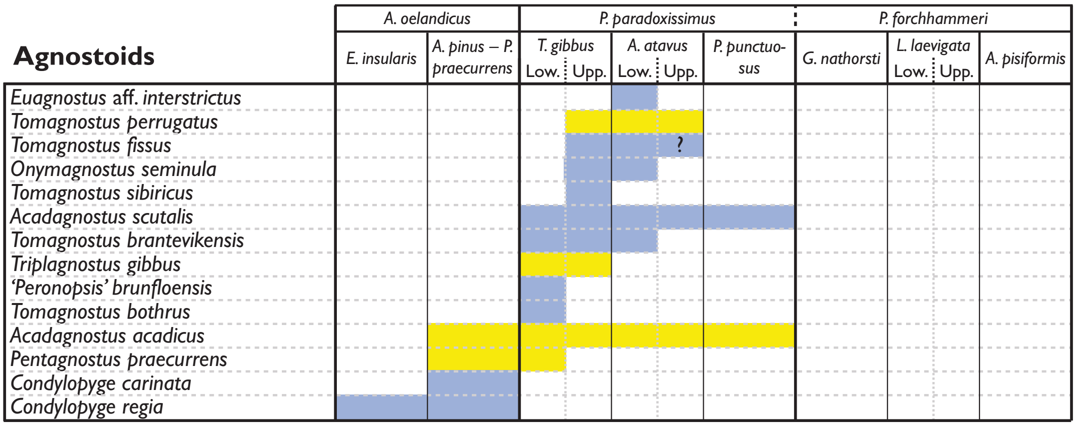
See References for complete citations.

Appendix 2. Range chart for all agnostoids and trilobites described from the Miaolingian of Scandinavia. Taxa in yellow occur in Lapland and elsewhere in Scandinavia, with the exception of *Eodiscus borealis* and *Cotalagnostus greilingi* n. sp., while taxa in blue do not occur in Lapland.

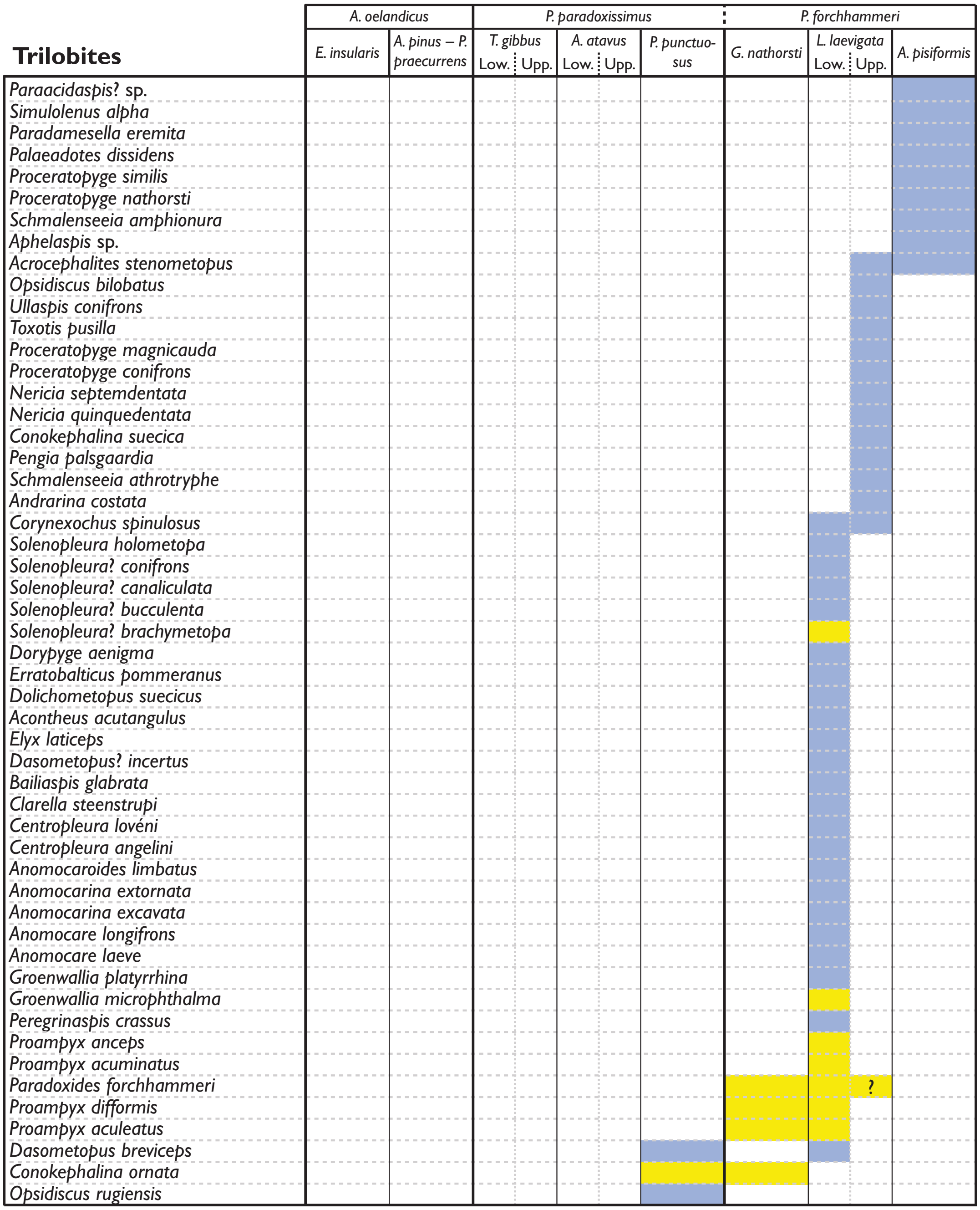


	A. oelandicus		*P. paradoxissimus*					*P. forchhammeri*			
Agnostoids	*E. insularis*	*A. pinus – P. praecurrens*	*T. gibbus*		*A. atavus*		*P. punctuosus*	*G. nathorsti*	*L. laevigata*		*A. pisiformis*
			Low.	Upp.	Low.	Upp.			Low.	Upp.	
Cristagnostus papilio											🟦
Peratagnostus falanensis											🟦
Agnostus pisiformis										🟨	🟨
Lisogoragnostus confluentus										🟨	
Glaberagnostus? forfex										🟦	
Glaberagnostus altaicus										🟦	
Clavagnostus spinosus										🟦	
Oidalagnostus trispinifer										🟦	
'Peronopsis' insignis										🟦	
Tomagnostella sulcifera										🟦	
Tomagnostella denticulata										🟦	
Lejopyge armata										🟦	
Goniagnostus spiniger										🟦	
Hypagnostus tjernviki									🟦 ?	🟦 ?	
Clavagnostus repandus									🟦	🟦 ?	
Glaberagnostus bituberculatus									🟨	🟨	
Diplagnostus planicauda vestgothicus									🟦	🟦	
Lejopyge laevigata									🟨	🟨	
Innitagnostus neglectus									🟦	🟦	
Oidalagnostus? dubius									🟦 ?		
Megagnostus glandiformis									🟨		
Linguagnostus kjerulfi									🟨		
Diplagnostus planicauda planicauda									🟦		
Cotalagnostus greilingi n. sp.									🟨		
Cotalagnostus confusus									🟨		
Hypagnostus brevifrons									🟨		
Homagnostus pater									🟨		
Acadagnostus minor									🟨		
Acidusus aculeatus								🟨	🟨		
Valenagnostus marginatus								🟨	🟨		
Oedorhachis? tricuspis								🟦	🟦		
Goniagnostus nathorsti								🟨	🟨		
'Agnostus' insularis								🟦			
Lejopyge calva								🟨			
Goniagnostus scanensis								🟦			
Acidusus? cassis								🟦			
Tomagnostella exsculpta							🟨 ?	🟨	🟨		
Glaberagnostus? cicer							🟨	🟨	🟨		
'Diplorrhina' quadrata							🟨		🟨		
Lejopyge lundgreni							🟨	🟨	🟨		
Doryagnostus incertus							🟨	🟨			
Megagnostus? resecta							🟦				
Linguagnostus groenwalli							🟦				
Lejopyge elegans							🟨				
Ptychagnostus punctuosus							🟦				
Diplagnostus planicauda bilobatus						🟨	🟨	🟨	🟨		
Onymagnostus hybridus						🟨	🟨	🟨			
Doryagnostus deltoides						🟨	🟨				
'Diplorrhina' cylindrica						🟦	🟦				
Svenax pusillus						🟦	🟦				
Cotalagnostus rotundus						🟦	🟦				
Hypagnostus truncatus						🟨	🟨				
Hypagnostus lingula						🟨	🟨				
Ptychagnostus affinis						🟨	🟨				
Pleuroctenium scanense						🟦					
Skryjagnostus pompeckji						🟦					
Acadagnostus aff. *bulkurensis*						🟦					
Phalagnostus ovalis						🟦					
Euagnostus? aff. *glandifer*						🟦					
Hypagnostus clipeus						🟨					
Onymagnostus mundus						🟦					
Acadagnostus ferox					🟨	🟨	🟨	🟨	🟨		
Condylopyge spinigera					🟦	🟦	🟦				
Phalagnostus scanicus					🟦	🟦	🟦				
Condylopyge rex					🟦	🟦	🟦				
Phalagnostus nudus					🟦	🟦	🟦				
'Diplorrhina' depressa					🟨	🟨	🟨				
Cotalagnostus lens					🟦	🟦	🟦				
Cotalagnostus claudicans					🟨	🟨	🟨				
Hypagnostus parvifrons					🟨	🟨	🟨				
Hypagnostus mammillatus					🟨	🟨	🟨				
Hypagnostus frontosa					🟦	🟦	🟦				
Onymagnostus ciceroides					🟦	🟦	🟦				
Acidusus atavus					🟨	🟨					

Taxa in yellow occur in Lapland and elsewhere in Scandinavia, with the exception of *Eodiscus borealis* and *Cotalagnostus greilingi* n. sp., while taxa in blue do not occur in Lapland. (Table continues on next page.)



Agnostoids	*A. oelandicus*		*P. paradoxissimus*					*P. forchhammeri*			
	E. insularis	*A. pinus – P. praecurrens*	*T. gibbus*		*A. atavus*		*P. punctuosus*	*G. nathorsti*	*L. laevigata*		*A. pisiformis*
			Low.	Upp.	Low.	Upp.			Low.	Upp.	
Euagnostus aff. *interstrictus*					🟦						
Tomagnostus perrugatus				🟨	🟨	🟨					
Tomagnostus fissus				🟦	🟦	🟦 ?					
Onymagnostus seminula				🟦	🟦						
Tomagnostus sibiricus				🟦							
Acadagnostus scutalis			🟦	🟦	🟦	🟦	🟦				
Tomagnostus brantevikensis			🟦	🟦	🟦						
Triplagnostus gibbus			🟨	🟨							
'Peronopsis' brunfloensis			🟦								
Tomagnostus bothrus			🟦								
Acadagnostus acadicus		🟨	🟨	🟨	🟨	🟨	🟨				
Pentagnostus praecurrens		🟨	🟨								
Condylopyge carinata		🟦									
Condylopyge regia	🟦	🟦									



Trilobites	*A. oelandicus*		*P. paradoxissimus*					*P. forchhammeri*			
	E. insularis	*A. pinus – P. praecurrens*	*T. gibbus*		*A. atavus*		*P. punctuosus*	*G. nathorsti*	*L. laevigata*		*A. pisiformis*
			Low.	Upp.	Low.	Upp.			Low.	Upp.	
Paraacidaspis? sp.											🟦
Simulolenus alpha											🟦
Paradamesella eremita											🟦
Palaeadotes dissidens											🟦
Proceratopyge similis											🟦
Proceratopyge nathorsti											🟦
Schmalenseeia amphionura											🟦
Aphelaspis sp.											🟦
Acrocephalites stenometopus										🟦	🟦
Opsidiscus bilobatus										🟦	
Ullaspis conifrons										🟦	
Toxotis pusilla										🟦	
Proceratopyge magnicauda										🟦	
Proceratopyge conifrons										🟦	
Nericia septemdentata										🟦	
Nericia quinquedentata										🟦	
Conokephalina suecica										🟦	
Pengia palsgaardia										🟦	
Schmalenseeia athrotryphe										🟦	
Andrarina costata										🟦	
Corynexochus spinulosus									🟦	🟦	
Solenopleura holometopa									🟦		
Solenopleura? conifrons									🟦		
Solenopleura? canaliculata									🟦		
Solenopleura? bucculenta									🟦		
Solenopleura? brachymetopa									🟨		
Dorypyge aenigma									🟦		
Erratobalticus pommeranus									🟦		
Dolichometopus suecicus									🟦		
Acontheus acutangulus									🟦		
Elyx laticeps									🟦		
Dasometopus? incertus									🟦		
Bailiaspis glabrata									🟦		
Clarella steenstrupi									🟦		
Centropleura lovéni									🟦		
Centropleura angelini									🟦		
Anomocaroides limbatus									🟦		
Anomocarina extornata									🟦		
Anomocarina excavata									🟦		
Anomocare longifrons									🟦		
Anomocare laeve									🟦		
Groenwallia platyrrhina									🟦		
Groenwallia microphthalma									🟨		
Peregrinaspis crassus									🟦		
Proampyx anceps									🟨		
Proampyx acuminatus									🟨		
Paradoxides forchhammeri								🟨	🟨	🟨 ?	
Proampyx difformis								🟨	🟨		
Proampyx aculeatus								🟨	🟨		
Dasometopus breviceps							🟦		🟦		
Conokephalina ornata							🟨	🟨			
Opsidiscus rugiensis							🟦				

Trilobites	*A. oelandicus*		*P. paradoxissimus*					*P. forchhammeri*			
	E. insularis	*A. pinus – P. praecurrens*	*T. gibbus*		*A. atavus*		*P. punctuosus*	*G. nathorsti*	*L. laevigata*		*A. pisiformis*
			Low.	Upp.	Low.	Upp.			Low.	Upp.	
Parasolenopleura? peregrina							🟦				
Nassovia globiceps							🟦				
Paradoxides davidis							🟦				
'Paradoxides' rugulosus of Grönwall							🟦				
'Paradoxides' rugulosus of Brøgger							🟦				
Mawddachites? brachyrhachis							🟦				
Dorypyge danica							🟦				
Holocephalina teres							🟦				
Ctenocephalus tumida							🟦				
Conocoryphe sulzeri							🟦				
Bailiella aequalis							🟦				
Clarella cf. *impar*							🟦				
Clarella groenwalli							🟦				
Centropleura angustata							🟦 ?				
Burlingia angusta							🟦				
Proampyx? depressus							🟦				
Paraxenocephalus mirus						🟦	🟦				
Solenopleura? nuntia						🟦	🟦				
Corynexochus bornholmiensis						🟦	🟦				
Meneviella venulosa						🟦	🟦				
Bailiella ornata						🟦	🟦				
Anopolenus henrici						🟦	🟦				
Hydrocephalus aff. *carens*						🟦	🟦				
Eodiscus punctatus						🟨	🟨				
Luhops expectans						🟦					
Clarella impar						🟦					
Burlingia jagoi					🟦	🟦	🟦				
Parasolenopleura spinigera					🟦	🟦	🟦				
Parasolenopleura linnarssoni					🟨	🟨	🟨				
Schmalenseeia acutangula					🟦	🟦	🟦				
Agraulos longicephalus					🟦	🟦	🟦				
Solenopleura? applanata					🟦						
Mawddachites hicksii					🟦						
Eodiscus scanicus					🟦						
Paradoxides paradoxissimus			🟨	🟨	🟨	🟨	🟨				
Parasolenopleura scanica			🟦	🟦	🟦	🟦					
Bailiella tenuicincta			🟦	🟦	🟦						
Paradoxides paradoxus			🟦 ?	🟦 ?							
'Paradoxides' palpebrosus			🟦	🟦							
Solenopleura? parva			🟦	🟦							
Solenopleura? munsteri			🟦	🟦							
Parasolenopleura aculeata			🟦	🟦							
Ellipsocephalus lejostracus			🟦	🟦							
Dorypyge oriens			🟦	🟦							
Ctenocephalus exsulans			🟦	🟦							
Bailiella impressa			🟦	🟦							
Bailiaspis dalmani			🟦	🟦							
Eodiscus borealis			🟨	🟨							
Paradoxides jemtlandicus			🟦								
Hydrocephalus cf. *carens*		🟦 ?	🟦 ?	🟦	🟦 ?	🟦					
Eccaparadoxides cf. *pusillus*		🟦 ?	🟦 ?	🟦	🟦 ?	🟦					
Ellipsocephalus cf. *hoffii*		🟦 ?	🟦 ?	🟦	🟦 ?	🟦					
Hydrocephalus vikensis		🟨									
Hydrocephalus spinulosus		🟦									
Dawsonia oelandica		🟦									
Eccaparadoxides? thorslundi		🟦									
Acadoparadoxides torelli		🟨									
Acadoparadoxides pinus		🟦									
Kootenia westergaardi		🟦									
Ellipsocephalus platys		🟦									
Burlingia hectori		🟦									
Acadoparadoxides bidentatus		🟦									
Macannaia skybergi		🟦									
Parasolenopleuea cristata	🟦 ?	🟦									
Hydrocephalus sjoegreni	🟦	🟦									
Acadoparadoxides quadrimucronatus	🟦	🟦									
Acadoparadoxides oelandicus	🟨	🟨									
Ellipsocephalus polytomus	🟦	🟦									
Eccaparadoxides insularis	🟦										
Bailiella froensis	🟦										
Bailiella emarginata	🟦										

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